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THE BIOLOGY OF FOMES FOMENTARIUS

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THE MAINE AGRICULTURAL EXPERIMENT STATION
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BULLETIN 409

THE BIOLOGY OF FOMES FOMENTARIUS[1]

M. T. Hilborn

INTRODUCTION

General observations by the author indicate that *Fomes fomentarius* is among the fungi that are most important in producing decay of hardwood trees, which comprise much of the 15,000,000 acres of Maine forests, and that it attacks birch more frequently than most other trees. Birch is abundant on more than 5,500,000 acres of Maine timberlands. Therefore a study of *F. fomentarius* might, it was thought, be of considerable economic importance.

During the past 20 years most of the pathologically important species in the genus *Fomes* have been the subject of rather intensive investigations. *F. applanatus* (Pers.) Wallr. has been studied by White (*88*), *F. pinicola* (Swartz) Cke. by Mounce (*54*), *F. pini* (Thore) Lloyd by Percival (*62*) and Owens (*61*), and *F. igniarius* (L.) Gill. by Verrall (*86*). Our knowledge of *F. fomentarius*, however, remains much as it was in 1889 [Hartig (*36, p. 178*)].

The purpose of the present investigation has been to study the biology of *F. fomentarius*. Certain phases seemed to demand special attention. For example, the recent literature has indicated that considerable variation exists within each of several species of the Hymenomycetes, including wood-rotting fungi, as within species of other groups of fungi. Also some European pathologists consider *F. fomentarius* to be a parasite, while in this country it is usually said to be a saprophyte. Finally, *F. fomentarius* has been considered to be entirely different from other species in the genus in regard to the formation and liberation of spores, the period of spore discharge, and the type of decay produced.

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[1] Part of a dissertation submitted to the Graduate School of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writer is indebted to Drs. J. S. Boyce, Donald Folsom, and F. B. Chandler for their advice and criticism during the progress of this work.

SYNONYMY

Probably because of its wide distribution and occurrence on many different hosts, *Fomes fomentarius* has been described under many names. In most mycological literature the fungus is cited as *Fomes fomentarius* (L.) Gill. Hilborn and Linder (*40*) give a partial list of synonyms, call attention to the work of Kickx published eleven years earlier than that of Gillet, and show that, according to the International Rules of Nomenclature, the fungus should be cited as *Fomes fomentarius* (Fr.) Kickx. The following list includes those names usually accepted as synonyms in mycological literature:

Boletus fomentarius L. Sp. Pl. 1176. 1753.

Boletus fomentarius L. Fl. Suecica (2nd ed.) p. 453. 1755.

Boletus ungulatus Bull. Champignons de France pp. 357-358. pl. 401, 491. 1791.

Boletus fomentarius Pers. (spelled "fomontarius") Obs. Myc. *2:* 1. 1799.

Boletus ungulatus var. *salicina* Pers. Obs. Myc. *2:* 4. 1799.

Boletus ungulatus var. *quercina* Pers. Obs. Myc. *2:* 4. 1799.

Boletus igniarius Sowerby English Fungi *2:* pl. 132. 1799.

Boletus fomentarius var. *ungulatus* Pers. Synops. Fung. p. 537. 1801.

Boletus fomentarius var. *prunastri* Alb. & Schw. Conspectus Fung. p. 252. 1805.

Boletus fomentarius var. *pomaceus* Alb. & Schw. Conspectus Fung. p. 252. 1805.

Boletus (Apus) fomentarius Pers. Nees, Syst. Pilze Schwämme. *2:* 57. 1817.

Polyporus fomentarius Fries Syst. Myc. *1:* 374. 1821.

Polyporus fomentarius Fries Epicrisis p. 465. 1836-38.

Polyporus fomentarius var. *excavatus* Berk. Ann. Soc. Nat. History *3:* 387. 1839.

Polyporus (Fomes) fomentarius Fries Summa Veg. Scand. p. 321. 1849.

Polyporus Inzengae DeNot. Erb. Critt. Ital. no. 636. 1860-61.

Fomes fomentarius (Fr.) Kickx Fl. Crypt. Flandres *2*: 237-238. 1867.

Fomes fomentarius (L.) Gill. Champ. Fr. *1:* 686. 1878.

Polyporus fomentarius var. *pomaceus* Berk & Br. Ann. Nat. Hist. V. *12:* 373. 1883.
Fomes Inzengae (DeNot.) Sacc. Syll. Fung. *6:* 175. 1888.
Fomes fomentarius (L.) Fries Sacc. Syll. Fung. *6:* 179-180 1888.
Placodes fomentarius Quel. Flore Mycol. p. 398. 1888.
Ochroporus fomentarius (L.) Schroeter Cohn, Krypt. Fl. Schlesien *3* (1) : 486. 1889.
Ungulina fomentaria (Fr.) Pat. Essai Tax. Hymen p.102. 1900.
Elfvingia fomentaria (L.) Murrill Bull. Torrey Bot. Club *30:* 298. 1903.
Elfvingiella fomentaria (L.) Murrill Northern Polypores, pub. by author, New York, 64 pp. 1914.
Polyporus (Ungulina) Inzengae DeNot. Biers, Bull. Soc. Path. Veg. France *9:* 166-168. 1922.

To this list Lloyd (*48*) would add the following: *Fomes introstuppeus* Cke., *F. marmoratus* Berk., *F. nigrescens* Klotzsch, *F. sclerodermeus* Lev., and *F. subfomentarius* Romell. At the present time it is inadvisable to include these in a list of synonyms until it has been possible to study type specimens.

Macdonald (*52*) studied *Fomes fomentarius* and its variety *nigrescens* in culture. Considerable variation was observed, but no character extended outside the range given by Fritz (*33*) in her cultural study of this species. According to Macdonald two superficially distinct types of sporophores, marking the extremes of the variations within this species, occur in Europe. In France, there is a rapidly growing soft form on beech. In northern Europe, there is a more slowly growing, harder, often darker type occurring on birch. Macdonald believes that Fries at the time of his original determination of *Polyporus nigricans*, regarded the southern form of *Polyporus fomentarius* as typical of the species and so gave the new name to the northern European type. As a result of his study Macdonald would add *Fomes nigricans* (Fr.) Gill. and *F. fomentarius* var. *nigrescens* (Klotzsch) Lloyd as synonyms of *Fomes fomentarius.*

DISTRIBUTION AND HOSTS

Fomes fomentarius is a widely distributed species, being reported from most of the North American Continent, the British Isles, northern and central Europe, China, Japan, and northern Africa. It has been reported in the literature and in the Bibliographical Index at the Farlow Herbarium, Harvard University, as occurring on 23 genera and 56 species. Of these genera 3 are conifers and the remainder are hardwood. In New England, however, field collections by the writer indicate that the fungus is practically restricted to *Betula* and *Fagus*, with only an occasional specimen occurring on other genera such as *Acer, Alnus, Quercus,* and *Ulmus*. In Maine the fungus is most commonly found on *Betula populifolia, B. lutea, B. papyrifera,* and *Fagus grandifolia,* and its abundance on these species is in decreasing order as listed here.

THE SPOROPHORE

The sporophore of *Fomes fomentarius* (see Plate 1) has been described by various writers. The following description is essentially the same as those given by Overholts (*59, 60*), and Lowe (*51*):

> Plants perennial, sessile; pileus woody, dimidate, convex to ungulate, 3-10 x 5-30 x 2-10 cm., covered with a thick crust, grayish to black, glabrous, margin thick and obtuse, sterile below; context dark brown, soft and punky, zonate, 0.3-3 cm. thick; tubes 0.3-2.5 cm. long, distinctly stratified, mouths grayish to brown, circular, averaging 3 per mm., the walls thick and entire, cystidia or setae none; spores hyaline, smooth, cylindric-ellipsoid, 12-27 x 4-11 microns.

The spores of *F. fomentarius* have been variously described by different authors. Murrill (*56*) in describing *Elfvingia fomentaria* reported the spores as being globose, smooth, very light brown, and 3-4 microns in diameter. Later Murrill (*57*) separated the genus *Elfvingiella* from *Elfvingia* by saying that the species with brown-colored spores belonged to *Elfvingia* and the species with hyaline-colored spores to *Elfvingiella*, with *E. fomentaria* being the type species. Overholts (*60*) records the spores of *F. fomentarius* as cylindric, hyaline, and 12-18 x 4-5 microns. Lowe (*51*) states

that the spores are cylindric-ellipsoid, and 12-16 x 4-5 microns. Bjørnekaer (*7*) found spore size to vary during the season. The spores discharged in the spring were larger, having an average length of 21 microns, as compared with those discharged later in the year which were 15 microns in length.

Measurements of spores discharged from sporophores in Maine showed the spores to be considerably larger than the previously reported figures. Their size did not vary much during the season. Spores discharged in the early part of the season, May to July, were essentially of the same size as those discharged in September. The range of 100 spores from a sporophore on white birch was 20.0-27.5 x 7.0-8.5 microns. Spores from a sporophore on gray birch were 19.5-25.0 x 10.0-11.5 microns. When analyzed in more detail these measurements are: from white birch, $25.45 \pm .142$ x $7.33 \pm .025$; from gray birch, $22.41 \pm .106$ x $10.34 \pm .126$ microns.

The stratified nature of the tubes and the production of spores have also been variously described in the literature. Overholts (*59*) stated that the hymenial tubes of *F. fomentarius* were "rather distinctly stratified." Later, however, Overholts (*60*) reported that the hymenial tubes were unstratified. Lowe (*51*) stated that the tubes were "rather distinctly stratified." The writer examined specimens representing field collections in New England, various herbaria of botanists, and exsiccatae at the Farlow Herbarium, Harvard University, Cambridge, Mass., and all showed the hymenial tubes to be stratified (see Plate 2).

Faull (*28*) states that *F. fomentarius* develops each new layer of hymenial tubes in the autumn but delays the production and liberation of spores from these tubes until spring. Faull also found that a fruiting body of this fungus will produce spores for 3 or 4 years from the same tube-layer. Thus a sporophore 4 years old would produce and liberate spores from the tubes of all 4 hymenial layers. Faull's work was described in more detail by Buller (*16, pp. 105-112*). Priehaüssen (*67*) also recorded that older portions of the fruiting body produced spores. However, if these observations were correct, this spore production would make *F. fomentarius* distinctly different from all other species in the genus because they usually form a sterile layer that seals the hymenial

tubes produced during the season's growth preventing further spore liberation from that layer of growth.

Therefore, specimens of *F. fomentarius* were collected in Maine during the spring and summer season of 1938 and examined microscopically. Difficulty was experienced in finding basidia by making free-hand sections, mounting in lacto-phenol, and staining in cotton-blue. Therefore material was embedded, sectioned, and stained by both the celloidin and paraffin methods as outlined by Chambrelain (*23*). The stratified nature of the tubes is very evident in microscopic sections. The ends of the tubes are sealed at the end of the year's growth by a sterile layer of rather thick-walled, brown hyphae much like the hyphae in the context. Basidia were found only in the current year's hymenial tube-layers and were completely absent in the earlier tube-layers.

Bjørnekaer (*7*) showed by marking the annual growth on a sporophore of *F. fomentarius* that each year it develops at least two distinct tube-layers, the one corresponding to the spring spore-production period and the other to the autumnal one. Between these two main tube-layers, small layers may be developed giving rise to short, summer spore, discharge periods. This is shown in Plate 2 in the last year's growth of a three-year-old sporophore.

In the course of the spore-discharge studies described in the following section, it was noticed that the underside of a sporophore would become lighter in color and very moist at least 2 to 3 weeks before spores were first discharged in the spring. This was because the hymenial tubes began to elongate in early spring, producing basidia and liberating spores shortly afterward.

Freeman (*32*) in discussing *F. fomentarius* stated that sporophores have been found that were 100 years old. Bjørnekaer (*7*) stated that there is no reliable foundation for reports that fruiting bodies live for more than 10 years. Field studies in New England, and particularly in Maine, have failed to reveal any sporophore more than 8 years in age.

SPORE DISCHARGE

References to the spore-discharge period and the factors influencing it indicate that considerable variation exists among the species of the genus *Fomes*. White (*88*) working with *F. appla-*

natus found that spore discharge began in May and continued until the first heavy frost in October or early November. A few spores were discharged during the winter. Percival (*62*) working with *Fomes pini* found that spores were discharged during every month of the year, but that only a few were discharged during the winter months. Buller (*16*) and Faull (*29*) state that the spore-discharge period of *F. fomentarius* is very short, beginning in the spring during the latter part of April and continuing until the end of May. Bjørnekaer (*7*) found that *F. fomentarius* discharged its spores from April to October and that the spore-discharge period exhibited two peaks, one in the spring and the other in the autumn. During the heat of the summer, spore discharge decreased or ceased. Buchwald (*15*) studied the spore discharge of *F. fomentarius* on a log of *Populus virginiana* in the laboratory. He found the spores to be discharged throughout the day and night with no indication of any periodicity. By wrapping a sporophore in oilcloth he was able to collect all the spores discharged during a definite time interval. These spores were suspended in water and the total number discharged was calculated by means of a haemocytometer. He found the spore production per hour to be about 2300 to 2500 millions, corresponding to about 55,000 to 60,000 millions in 24 hours. According to Buchwald a sporophore of medium size would discharge 50,000 to 100,000 millions of spores in 24 hours. Applying these figures to the spore-fall period of 180 days as determine by Bjørnekaer, Buchwald calculated that a single, medium-sized sporophore of *F. fomentarius* would discharge the astounding total of 9,000 to 18,000 billions (milliards) of spores during one season.

Meyer (*53*) determined the weight of one spore of *F. fomentarius*. She weighed the total spore discharge that occurred in the laboratory from March 25 to April 13, inclusive, finding that a total of 1,115 grams of spores were discharged. By calculating the volume of one spore and assuming its specific gravity to be the same as water, she calculated the weight of one spore to be 0.000 000 000 146 grams. In dividing this number into the 1,115 grams of spores, she obtained the figure 7,563,493,150 as the number of spores discharged during the 20-day interval. This figure is incorrect, as 1,115 divided by 0.000 000 000 146 is 7,636,986,301,369 spores. Thus the average daily discharge of

the single fruiting body for the 20 days was 318,207,762,557 spores, and not the figure 378,424,655 (*sic*) spores as reported by Meyer. Buchwald by means of his haemocytometer counts found one spore of this species to weigh 0.000 000 000 111 grams. If this figure is multiplied by the 18,000 billions of spores as discharged during the 180-day interval the total weight of the spores discharged is 1,998 grams. The average daily rate of spore production of the sporophore studied by Buchwald was 100 billions of spores while the sporophore studied by Meyer discharged spores at a rate of 318 billions per day. This difference in rate of production may be accounted for by the fact that the sporophore studied by Meyer was placed near a radiator; the heat may have stimulated spore production. From these figures it is apparent that the spore production of *F. fomentarius* is in excess of any other reported figure in the *Hymenomycetes*. White (*88*), for example, found that *F. applanatus* discharged 30 billions of spores in 24 hours. It is interesting to note that an average-sized sporophore of *F. fomentarius* weighs approximately 130 grams. Assuming Buchwald's figures of 1988 g. of spores to be the amount produced by such a sporophore, it is evident that a sporophore could produce about 15 times its own weight in spores during one season.

Considerable variation in the rate of spore discharge from time to time exists in various *Hymenomycetes*. Hirt (*41*) working with *Polyporus gilvus* found that spore discharge for all sporophores under observation started as early as July 2 and continued until the middle of August, but that the spore-discharge period for any given sporophore was much shorter. Later Hirt (*42*) found that *Trametes suaveolens* discharged spores during October, November, and early December and during the first warm days of spring. White (*88*) found, however, that the spore discharge of *F. applanatus* was not characterized by any diurnal or seasonal periodicity. Percival (*62*) noted that *F. pini* showed two brief periods of heavy spore discharge, but no daily periodicity was shown. Hirt (*41*) found that *Polyporus gilvus* discharged spores much more abundantly during the night than during the day. This discharge seemed to be independent of temperature. Later Hirt (*42*) in studying the spore discharge of *Trametes suaveolens* found that alternate periods of high and low temperature seemed to be the principal factor governing the discharge of spores. White

(*88*) found no influence of either temperature or humidity on the spore discharge of *F. applanatus*. Percival (*62*) found temperature to be the major influence in determining periods of spore discharge. His data are based on weekly averages. Spore discharge occurred at all times except when the weekly temperature was below 32° F. Heavy spore discharge resulted from a period of cool weather followed by a rise in temperature above 50° F. Buchwald (*15*) found that when a sporophore of *F. fomentarius* was cooled down from 6 to 4 degrees C. in 24 hours its spore discharge was reduced markedly.

In order to study the spore-discharge period of *F. fomentarius* and to determine the meteorological factors influencing it, field studies were conducted during 1938 and 1939. Spore traps were constructed in the vicinity of Orono, Maine, on 5 gray birch trees in 1938 and on 9 gray birch trees in 1939. These spore traps were made of tin cans carefully fitted around a sporophore on a standing tree. A glass slide, coated with vaseline, was placed 1 cm. beneath each sporophore. These glass slides were so marked that each was replaced in exactly the same position in regard to the pore openings when the slides were changed. The slides were examined daily under a microscope. At each examination, five fields were located on each slide by means of a mechanical stage. The spores in each of these five fields were counted and averaged. At the time that the slides were changed the temperature and relative humidity were determined by means of a sling psychrometer. Approximately 500 spores completely filled the microscopic field, and occasionally during the peak of spore production the spore deposit on a slide would be too thick to make accurate counts. In this case the number of spores was assumed to be just 500, as it was necessary to have a definite figure for further calculations.

In 1938, spore discharge began on April 15 and continued until July 7. It began again on August 27 and continued until September 25. The 1939 data showed approximately the same periodicity. In 1939 the work had to be discontinued during most of May and as a result the data for 1939 are not as complete as the 1938 data. Thus in all further discussion the data for 1938 are used. When the spore-discharge index, humidity, and temperature were plotted, many sharp increases and decreases were shown. These were smoothed out by means of a 5-day moving average.

The resulting data are presented in fig. 1. The number of spores represents the average of 5 microscopic fields on each of 5 spore traps, and is therefore just an extremely small portion of the total number on each slide. No attempt was made to determine the total number of spores discharged by an individual sporophore.

From fig. 1 it is apparent that the spore-discharge period can be divided into three intervals, the pre-peak, peak, and post-peak. The pre-peak interval extended from approximately April 15 to May 22, the peak interval from May 23 to June 19, and the post-peak interval from June 20 to September 25. In order to study the effects of meteorological stimuli on spore discharge, the data during each of these intervals were analyzed in detail. Correlation coefficients were calculated using the data obtained by means of a 5-day moving average. These figures are shown in table 1. It is apparent that, during the pre-peak interval, humidity is an

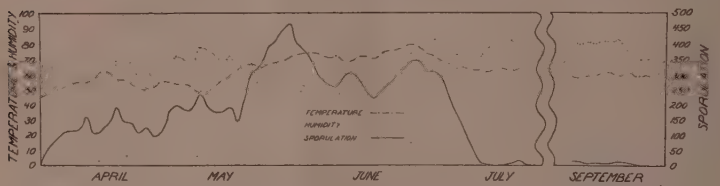

FIG. 1. Temperature, humidity, and seasonal spore discharge of *Fomes fomentarius*. Sporulation data are based on 5 spore traps. All data presented have been smoothed out by means of a 5-day moving average.

TABLE 1

Correlation Coefficients for Temperature and Relative Humidity vs. Number of Spores of Fomes fomentarius Discharged During Different Parts of the Sporulation Period Using the 5-day Moving Average Data

Sporulation period	r for temperature vs. spores	r for relative humidity vs. spores
Pre-peak	+.368 (significant)[1]	+.514 (significant)
Peak	−.501 (significant)	−.352 (not significant)
Post-peak	+.922 (highly significant)	−.260 (not significant)

[1] Significance based upon Wallace, H. A., and G. W. Snedecor, Correlation and machine calculation. Iowa State Col. Agr. Mech. Arts Off. Pub. Vol. 30, No. 4. 1931.

important factor governing spore discharge, and that temperature is a significant factor during the entire period of spore discharge, and becomes highly significant during the post-peak interval.

From these data it can be concluded that *F. fomentarius* has a spore discharge period of approximately 180 days as reported by Bjørnekaer (*7*). Temperature is an influencing factor on spore discharge and is most important during the post-peak interval. Atmospheric humidity is an influencing factor only during the pre-peak interval and has no influence on spore discharge during either the peak or post-peak intervals. Possibly the food reserves of the sporophore influence spore discharge during the peak interval.

GENERAL CULTURAL STUDIES WITH ARTIFICIAL MEDIA

Variations among monosporous and polysporous isolates of wood-rotting and other fungi have been reported by many investigators. Schmitz (*79*) found definite physiological and morphological differences between 4 isolates of *Fomes pinicola,* and concluded that in this species physiological variation existed which might be the result of host influence. Mounce (*54*) worked with the same fungus and found that isolates from different sources differed from one another in rate of growth, color production, and texture of mycelial mat. She concluded that these differences were the result of individual variation rather than the result of host influence. Later Mounce and Macrae (*55*) reported that monosporous isolates of *F. pinicola* from various countries could be divided into three groups: those from North America formed groups A and B, and those from France, Sweden, Germany, and Japan formed group C. Isolates from group A were compatible with each other; similarly, isolates from group B were mutually compatible; but isolates from group A were almost completely incompatible with those from group B. Group C isolates were completely compatible among themselves, almost completely compatible with those from group A, and only partially compatible with those in group B. Owens (*61*) worked with *F. pini* and found that the isolate of this fungus from *Abies grandis* was distinct from those growing on species of *Pinus, Pseudotsuga, Tsuga,*

Picea, and *Larix*, and other species of *Abies*. Verrall (*86*) investigated *F. igniarius* and found that the isolates of this species fell into three distinct groups, one group occurring on *Populus*, another group on *Betula*, especially *B. papyrifera*, and the third group on species of other genera and on some species of *Betula*. Childs (*24*) worked with *Polyporus schweinitzii* and found no evidence of local or host-specialized strains within this species, but found that different isolates varied from one another in appearance in culture, production of sporophores, growth rate on nutrient media, reaction to acidity, and apparent ability to cause decay of wood.

Childs further pointed out that any investigation of a species which is highly heterozygous, such as *F. fomentarius* may be assumed to be, should include a sufficient number of individuals to permit an approximate determination of the range of variability and the specific average.

Isolates and Media

As a result of the work reviewed above, a series of cultural studies on various media were planned. The isolates used in this study were obtained from various sources. Table 2 lists the isolates used, their sources, and the dates of isolation, when known. The media used in this work were as follows: Beef extract agar containing 0.2 per cent soluble starch, corn-meal agar, Czapek's medium, dextrose agar, gallic acid medium, lactose agar, Leonian's malt extract agar, lima bean agar, malt agar, maltose agar, potato dextrose agar, string bean agar, synthetic agar, and tannic acid medium. All cultures were incubated in darkness in a constant temperature chamber at 22° C.

Seven isolates of *F. fomentarius* from various hosts were grown on 10 of these media. These isolates were cultured in petri dishes in duplicate. Notes were made on the radial growth in millimeters at the end of 3, 6, 9, and 12 days. Various characteristics of the mycelial mat were noted at the end of 12 and 16 days. In describing these mycelial characteristics the terms given in the glossaries of Long and Harsh (*49*) and Campbell (*17*) were used. All colors noted were standardized by comparison with those of Ridgway (*73*).

TABLE 2

Source of Isolates of Fomes fomentarius

Isolate	Original source
F 1	Tissue culture from a sporophore on *Betula populifolia,* Orono, Maine. May, 1937.
F 4	Tissue culture from a sporophore on *Ulmus americana,* Newport, Maine. June, 1937.
F 6	Tissue culture from a sporophore on *Betula lutea,* Sebago Lake, Maine. June, 1937.
F 9	Tissue culture from a sporophore on *Ulmus americana,* Newport, Maine. June, 1937.
F 10	Tissue culture from a sporophore on *Betula papyrifera,* Bethel, Maine. July, 1937.
F 102[1]	"Culture from *Betula* sp., Scotland."
F 103	"Culture from *Betula* sp., Scotland."
F 105	"Culture of *F. fomentarius* var. *nigrescens* from *Betula* sp., Scotland."
F 111	"Culture from *Fagus* sp., Austria."
F 196[2]	Unknown.
F 197	Unknown.
F 206	Unknown.
F 1307[3]	"Culture from a sporophore on *Fagus grandifolia,* Ottawa, Ontario. May, 1930."
F 2252	"Tissue culture from a sporophore on *Betula* sp., Victoria Beach, Manitoba. May, 1932."
F 3309	"Culture from *Fraxinus americana,* England, Welch isolation. Culture received May, 1933 from W. P. K. Findlay. Ref. No. 79A."
17041-s[4]	"Transmitted by W. A. Campbell, State College, Pa. L. O. Overholts collection."
57081-s	"*Betula papyrifera,* Stone Valley, Pa. Feb., 1933. Overholts & Davidson."
58564-s	"*Fagus* sp., Jaffrey, N. H., Feb., 1934. C. S. Moses."
58572-s	"*Betula papyrifera,* Itasca Co., Minn. L. L. Sluzalis."
59009-s	"*Populus sp.,* Cloquet, Minn. June, 1934. C. Christensen."
59010-s	"*Populus tremuloides,* Cloquet, Minn. June, 1934. C. Christensen."

[1] F 102 to F 111 inclusive were received from Dr. J. A. Macdonald, The University, St. Andrews, Scotland, in October, 1939.

[2] F 196 to F 206 inclusive were received from Dr. J. Liese, Botanisches Institut, Forstliche Hochschule, Eberswalde bei Berlin, Germany, in October, 1939.

[3] F 1307 to F 3309 inclusive were received from Dr. Irene Mounce, Central Experimental Farms, Ottawa, Canada, in June, 1937.

[4] 17041-s to 71070 inclusive were received from Dr. R. W. Davison, Division of Forest Pathology, Bureau of Plant Industry, Washington, D. C., in July, 1937.

TABLE 2—(Concluded)

Isolate	Original source
59011-s	"*Betula papyrifera,* Cloquet, Minn. June, 1934. C. Christensen."
59012-s	"*Betula papyrifera,* Cloquet, Minn. June, 1934. C. Christensen."
59013-s	"*Betula papyrifera,* Cloquet, Minn. June, 1934. C. Christensen."
59100-s	"*Betula papyrifera,* Liberty, Maine. Sept., 1934. T. J. Grant."
70957	"*Acer* sp., Nicolet National Forest, Wisconsin, Nov., 1935. R. C. Lorenz."
70960	"*Betula lutea,* Nicolet National Forest, Wisconsin. Nov., 1935. R. C. Lorenz."
71070	"Birch Park Falls, Wisconsin. April, 1936. R. C. Lorenz."

Beef extract agar with 2 per cent soluble starch. All isolates except F 3309 made a thick cottony, woolly, or somewhat appressed, usually homogeneous growth. Cottony tufts of aerial mycelium appeared in F 10 and F 1307. The color varied from white to a pale gull gray or hyaline. F 3309 produced a thin, sparse, fimbriate growth.

Corn-meal agar. All isolates except F 1 produced a thin, appressed mycelium, usually white or a pale gull gray in color. F 6 produced a fawn color in the central zone; F 10 an avellaneous color in the central zone; and F 1307 a vinaceous color in the marginal zone. Cottony masses of aerial mycelium appeared in F 1307, and occasional tufts of aerial mycelium were produced in F 3309. F 1 made a thin, mostly appressed growth, with occasional tufts of aerial mycelium and produced an avellaneous color in the marginal zone (see Plate 3, B).

Czapek's medium. All isolates produced a thin, sparse, appressed growth, usually hyaline, but in F 10 a wood brown color appeared in the central zone, varying to a pale gull gray in the marginal zone.

Dextrose agar. All the isolates, except F 10, produced a thin, appressed, usually cobwebby growth that was either hyaline or a pale gull gray in color. The mat was fimbriate in F 1 and F 3309. F 10 produced a fairly thick mycelium.

Lactose agar. All the isolates produced a very thin, sparse, appressed growth that was fimbriate in F 3309. Color varied from hyaline or almost so in all except F 4 where a buckthorn brown appeared in the central zone.

Leonian's malt extract agar. All the isolates, except F 3309, produced a fairly thick, velvety, felty, or woolly growth which was somewhat appressed in F 1307 and F 2252. Color varied considerably. In color F 1 was almost indistinguishable from the color it produced on corn-meal agar, while F 4 was an army brown, F 6 ochraceous-tawny, and F 10 a wood brown. F 6 tended to be somewhat fimbriate, and F 1307 had occasional tufts of aerial mycelium scattered over a somewhat appressed mat. F 2252 produced a cobwebby growth. F 3309 produced a thin, appressed mycelium with occasional tufts of aerial mycelium (see Plate 4, A).

Lima bean agar. All the isolates, except F 3309, produced a rather thick, woolly, felty, or velvety growth, usually white to a pale gull gray in color. F 6, however, was vinaceous-buff in the central zone. The mycelium was plumose in F 1 and F 1307, and occasional tufts of aerial mycelium appeared in F 4, F 6, and F 10. F 3309 produced a rather thin, appressed mycelium (see Plate 3, D, and Plate 5).

Maltose agar. All the isolates produced a thin, appressed, sparse mycelium which was cobwebby in F 1 and F 1307, and with occasional tufts of aerial mycelium in F 10. Color varied from hyaline to white or a pale gull gray in all except F 6 where a fawn color appeared in the central zone (see Plate 3, C).

Potato dextrose agar. All the isolates, except F 3309, produced a thick, felty mycelium which was rather thin and somewhat appressed in F 1307 and thin and silky in F 3309. In F 4 the mycelium was cottony and fimbriate. F 1, F 4, and F 3309 were white or a pale gull gray in color, while F 6 was cinnamon brown, F 10 and F 2252 were ochraceous-tawny and F 1307 was ochraceous-buff.

Synthetic agar. All the isolates produced a thin, somewhat appressed, cobwebby, subfelty, or cottony growth which was either a pale gull gray or hyaline except in F 1307 where a vinaceous-buff color appeared.

It is apparent that there is considerable variation in the type of mycelial growth of the various isolates on the 10 media used.

However, the range of characters, while great, did not exceed those reported by previous investigators. The mat formed was usually thin and appressed, with no pore surfaces or vesicular bodies being formed; characteristics which Campbell (*17*) found were typical of *F. fomentarius*.

The comparative growth rates of these isolates are shown graphically in fig. 2. It is evident that there was considerable difference between these isolates in the rate of growth on the various media. The data obtained on comparative growth rates were analyzed by the analysis of variance method. Tables 3, 4, 5, and 6 show the data when analyzed at each of the 4-time intervals, i.e., 3, 6, 9, and 12 days. All the data are combined in table 7.

When the differences required for significance in tables 8 to 11 inclusive are compared with the differences between means of isolates, it is apparent that considerable variation exists.

F 1 differed significantly at 3 days only from F 3309; at 6 days from F 4, F 1307, and F 3309; at 9 days from all isolates

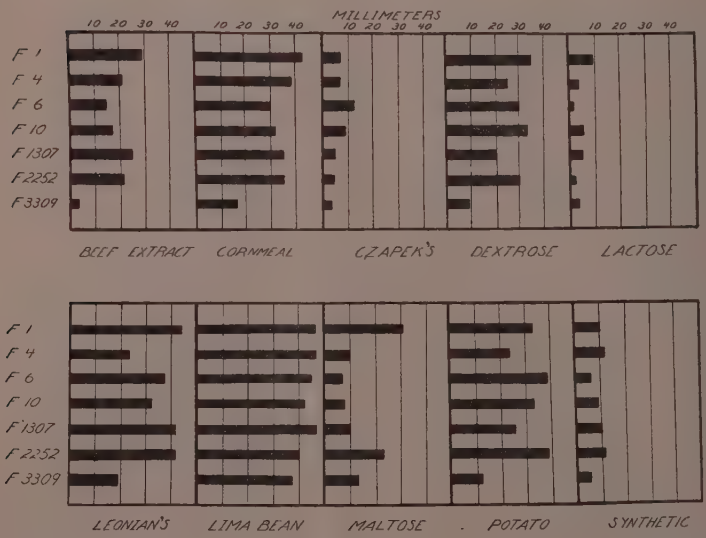

FIG. 2. Comparative radial growth rates at end of 12 days of various isolates of *Fomes fomentarius* on different substrata.

except F 2252; and at 12 days from all isolates. In all these differences F 1 made more growth than all the other isolates.

F 4 differed significantly at 3 days from F 10 and F 2252; at 6 and 9 days from F 1, F 10, F 2252, and F 3309; and at 12 days only from F 1 and F 3309. In all these differences F 4 made less growth than all the other isolates except F 3309.

F 6 differed significantly at 3 days only from F 3309; at 6 days from F 2252 and F 3309; and at 9 and 12 days from F 1 and F 3309. In these differences F 6 made less growth than all the other isolates except F 3309.

F 10 differed significantly at 3 days from F 4, F 1307, and F 3309; at 6 days from F 4, F 1307, and F 3309; at 9 days from F 1, F 4, F 1307, and F 3309; and at 12 days only from F 1 and F 3309. In these differences F 10 made more growth than all the other isolates except F 3309.

F 1307 differed significantly at 3 days from F 10 and F 2252; at 6 and 9 days from F 1, F 10, F 2252, and F 3309; and at 12 days only from F 1 and F 3309. In these differences it made less growth than all the other isolates except F 3309.

TABLE 3

Analysis of Variance of Radial Growth in Millimeters after 3 Days Incubation of 7 Isolates of F. fomentarius on 10 Media

Isolate	Media											
	Beef extract agar	Corn-meal agar	Czapek's medium	Dextrose agar	Lactose agar	Leonian's malt extract	Lima bean agar	Maltose agar	Potato dextrose agar	Synthetic agar	Sum of 10 media	Average[1]
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
F 1	1	5	0	4	0	4	2	0	0	1	17	1.7
F 4	2	3	0	2	0	2	2	0	0	0	11	1.1
F 6	1	3	0	2	0	5	1	0	6	1	19	1.9
F 10	2	3	0	6	0	4	2	0	7	1	25	2.5
F 1307	1	1	0	1	1	1	2	0	2	2	11	1.1
F 2252	2	6	0	3	0	3	2	0	5	2	23	2.3
F 3309	0	2	0	1	0	0	1	0	1	0	5	0.5
Sum	9	23	0	19	1	19	12	0	21	7	111	
Average[2]	1.3	3.3	0	2.7	0.1	2.7	1.7	0	3.0	1.0		1.6

[1] Difference required for significance = 1.00
[2] Difference required for significance = .82

TABLE 4

Analysis of Variance of Radial Growth in Millimeters After 6 Days Incubation of 7 Isolates of F. fomentarius on 10 Media

Isolate	Media										Sum of 10 media	Average[1]
	Beef extract agar	Corn-meal agar	Czapek's medium	Dextrose agar	Lactose agar	Leonian's malt extract	Lima bean agar	Maltose agar	Potato dextrose agar	Synthetic agar		
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
F 1	7	10	0	9	1	12	12	3	15	4	73	7.3
F 4	5	11	0	6	1	6	6	2	7	4	48	4.8
F 6	5	6	3	6	0	11	8	1	16	4	60	6.0
F 10	4	12	1	8	0	10	7	1	20	6	69	6.9
F 1307	3	6	0	3	2	11	8	1	12	6	52	5.2
F 2252	5	13	0	8	1	8	10	3	22	7	77	7.7
F 3309	0.5	5	0	3	2	6	7	1	7	1	32.5	3.3
Sum	29.5	63	4	43	7	64	58	12	99	32	411.5	
Average[2]	4.2	9.0	0.6	6.1	1.0	9.1	8.3	1.7	14.1	4.6		5.9

[1] Difference required for significance = 1.78
[2] Difference required for significance = 1.42

TABLE 5

Analysis of Variance of Radial Growth in Millimeters After 9 Days Incubation of 7 Isolates of F. fomentarius on 10 Media

Isolate	Media										Sum of 10 media	Average[1]
	Beef extract agar	Corn-meal agar	Czapek's medium	Dextrose agar	Lactose agar	Leonian's malt extract	Lima bean agar	Maltose agar	Potato dextrose agar	Synthetic agar		
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
F 1	18	25	3	20	7	30	31	17	24	9	184	18.4
F 4	11	26	4	14	2	12	25	7	9	7	117	11.7
F 6	8	18	9	17	0.5	24	25	4	26	5	136.5	13.7
F 10	12	25	6	21	2	24	22	3	29	7	151	15.1
F 1307	8	17	1	9	3	26	29	4	15	8	120	12.0
F 2252	11	27	3	19	2	20	30	9	29	10	160	16.0
F 3309	1	10	1	5	3	14	19	7	9	3	72	7.2
Sum	69	148	27	105	19.5	150	181	51	141	49	940.5	
Average[2]	9.9	21.1	3.9	15.0	2.8	21.4	25.9	7.3	20.1	7.0		13.4

[1] Difference required for significance = 3.2
[2] Difference required for significance = 2.6

TABLE 6

Analysis of Variance of Radial Growth in Millimeters After 12 Days Incubation of 7 Isolates of F. fomentarius on 10 Media

Isolate	Media										Sum of 10 media	Average[1]
	Beef extract agar	Corn-meal agar	Czapek's medium	Dextrose agar	Lactose agar	Leonian's malt extract	Lima bean agar	Maltose agar	Potato dextrose agar	Synthetic agar		
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
F 1	29	43	6	35	9	44	47	31	33	10	287	28.7
F 4	21	38	6	25	3	23	47	10	28	12	213	21.3
F 6	15	30	12	30	1	37	45	7	38	6	221	22.1
F 10	17	32	8	33	5	33	43	8	33	8	220	22.0
F 1307	24	35	4	15	5	41	47	10	25	10	216	21.6
F 2252	21	35	4	30	2	41	40	23	38	11	245	24.5
F 3309	3	16	3	8	4	18	37	13	12	5	119	11.9
Sum	130	229	43	176	29	237	306	102	207	62	1521	
Average[2]	18.6	32.7	6.1	25.1	4.1	33.9	43.7	14.6	29.6	8.9		21.7

[1] Difference required for significance = 4.4
[2] Difference required for significance = 3.6

TABLE 7

Analysis of Variance of Radial Growth in Millimeters of 7 Isolates of F. fomentarius on 10 Media

Sources of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	279	38848.59		
Between means of media	9	10948.76	1216.53	143.8
Between means of isolates	6	1680.06	280.01	33.1
Between means of 3-day growth intervals	3	16466.15	5488.72	648.8
Interactions:				
Media —isolates	54	1628.64	301.60	35.6
Media —growth interval	27	5927.22	219.52	25.9
Isolates—growth intervals	18	826.64	45.92	5.4
Error	162	1371.12	8.46	

F 2252 differed significantly at 3 days from F 4, F 1307, and F 3309; at 6 days from F 4, F 6, F 1307, and F 3309; at 9 days from F 4, F 1307, and F 3309; and at 12 days only from F 1 and F 3309. In these differences it made more growth than all the other isolates except F 1.

F 3309 differed significantly at 3 days from F 1, F 6, F 10, and F 2252; and at 6, 9, and 12 days from all other isolates. In these differences it made less growth than all the other isolates.

From these data it may be concluded that there is considerable variation in the time-growth curve for these isolates. More significant differences occurred between the isolates at the 6 and 9 day time-intervals. At the 12 day time-interval many of the differences had disappeared, apparently due to an adjustment of this time-growth factor.

The influence of media on variation in comparative growth rates is striking. Following are the differences between media in regard to their influence upon mycelial growth.

Beef extract agar differed significantly at 3 days from all media except lima bean and synthetic; at 6 days from all except synthetic; at 9 days from all except maltose and synthetic; and at 12 days from all except maltose. In all these differences it produced more growth than Czapek's, lactose, maltose, and synthetic, and less growth than corn meal, dextrose, Leonian's, lima bean, and potato dextrose.

Corn-meal agar differed significantly at 3 days from all media except dextrose, Leonian's, and potato dextrose; at 6 days from all except Leonian's and lima bean; at 9 days from all except Leonian's and potato dextrose; and at 12 days from all except Leonian's. In all these differences at 3 days corn meal produced more growth than all the other media; at 6 days more than all except potato dextrose; and at 9 and 12 days more than all except lima bean.

Czapek's medium differed significantly at 3 days from all media except lactose, maltose, and synthetic; at 6 days from all except lactose and maltose; and at 9 and 12 days from all except lactose and synthetic. In all these differences it produced less growth than all the other media.

Dextrose agar differed significantly at 3 days from beef extract, Czapek's, lactose, maltose, and synthetic; at 6 days from all except synthetic; and at 9 and 12 days from all other media. In these differences at 6, 9, and 12 days it produced more growth than all other media except corn meal, Leonian's, lima bean, and potato dextrose.

Lactose agar differed significantly at 3 days from all media

except Czapek's, maltose, and synthetic; at 6 days from all except Czapek's and maltose; and at 9 and 12 days from all except Czapek's. In all these differences it consistently produced less growth than all the other media.

Leonian's malt extract agar differed significantly at 3 days from all except corn meal, dextrose, lima bean, and potato dextrose; at 6 days from all except corn meal and lima bean; at 9 days from all except corn meal and potato dextrose; and at 12 days from all except corn meal. In these differences at 6 days it produced less growth than potato dextrose, and at 9 and 12 days less than lima bean.

Lima bean agar differed significantly at 3 days from all media except beef extract, dextrose, Leonian's, and synthetic; at 6 days from all except corn meal and Leonian's; and at 9 and 12 days from all media. In these differences at 3 days it produced less growth than corn meal and potato dextrose; at 6 days less than potato dextrose; and at 9 and 12 days it produced more growth than all the other media.

Maltose agar differed significantly at 3 days from all media except Czapek's, lactose, and synthetic; at 6 days from all except Czapek's and lactose; at 9 days from all except beef extract and synthetic; and at 12 days from all except beef extract. In these differences it produced less growth than all media except at 9 days when it produced more than Czapek's and lactose, and at 12 days more than these two and also synthetic.

Potato dextrose agar differed significantly at 3 days from all media except corn meal, dextrose, and Leonian's; at 6 days from all; at 9 days from all except lima bean; and at 12 days from all except corn meal and Leonian's. In these differences it produced more growth than all the media except lima bean at 9 and 12 days.

Synthetic agar differed significantly at 3 days from corn meal, dextrose, Leonian's, and potato dextrose; at 6 days from all except beef extract and dextrose; at 9 days from all except beef extract and maltose; and at 12 days from all except Czapek's. In these differences it produced less growth than all except Czapek's, lactose, and maltose at 6 days; Czapek's and lactose at 9 days; and lactose at 12 days.

The influence of both the source of isolate and of medium in causing variation in comparative growth rates is shown when the

F values in tables 3 to 6 are calculated. In all cases the values for F exceed the 1 per cent point of significance; i.e., the probability that the differences observed are due to chance is less than 1 in 100.

The relative influence of source of isolate and medium in causing variation in comparative growth rates is shown in table 7. The large F values show that all sources of variation are very highly significant, and the mean squares when compared exceed

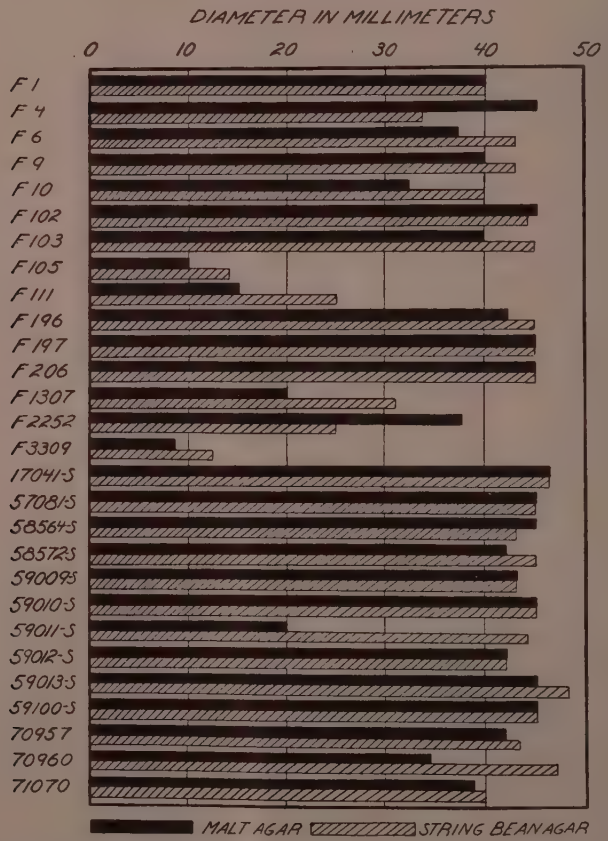

FIG. 3. Comparative radial growth rates at end of 12 days of 28 isolates of *Fomes fomentarius* on malt and string bean agars.

the 0.1 per cent point in Fisher's tables of Z; i.e., the probability that the differences observed are due to chance is less than 1 in 1000. A comparison of the mean squares between means of isolates and means of media shows that more variation in growth has been caused by media than by the isolates, as the F value for this comparison is 4.34 which is significant at the 5 per cent level.[2] This is equivalent to odds of 19:1.

Preliminary cultural work indicated that there was a great range of cultural characteristics produced on string bean agar. As a result all the isolates were compared on this agar. They were also compared on malt agar, as it is one of the most common stock media for wood-destroying fungi. The methods used in culturing and in obtaining data were similar to the previously described

TABLE 8

Analysis of Variance of Radial Growth in Millimeters After 3 Days Incubation of 28 Isolates of F. fomentarius on 2 Media

Isolate	Radial growth in millimeters at 3 days on		Average[1]
	Malt agar	String bean agar	
F 1	6	1	3.5
F 4	0	1	0.5
F 6	5	2	3.5
F 9	0	6	3.0
F 10	5	6	5.5
F 102	1	3	2.0
F 104	5	5	5.0
F 105	0	1	0.5
F 111	1	1	1.0
F 196	3	2	2.5
F 197	3	2	2.5
F 206	3	3	3.0
F 1307	2	2	2.0
F 2252	5	1	3.0
F 3309	0	1	0.5
17041-s	4	6	5.0
57081-s	4	8	6.0
57564-s	2	5	3.5
58572-s	4	7	5.5
59009-s	1	0	0.5
59010-s	6	5	5.5
59011-s	2	5	3.5
59012-s	2	6	4.0
59013-s	2	6	4.0
59100-s	8	8	8.0
70957	5	0	2.5
70960	6	7	6.5
71070	5	5	5.0

[1] Difference required for significance = 3.8

[2] $\frac{1216.53}{280.01} = 4.34$

TABLE 9

Analysis of Variance of Radial Growth in Millimeters After 6 Days Incubation of 28 Isolates of F. fomentarius on 2 Media

Isolate	Radial growth in millimeters at 6 days on		Average[1]
	Malt agar	String bean agar	
F 1	14	15	14.5
F 4	10	7	8.5
F 6	11	17	14.0
F 9	6	20	13.0
F 10	15	20	17.5
F 102	14	13	13.5
F 103	21	19	20.0
F 105	2	3	2.5
F 111	6	9	7.5
F 196	17	16	16.5
F 197	13	17	15.0
F 206	18	21	19.5
F 1307	6	10	8.0
F 2252	12	3	7.5
F 3309	1	2	1.5
17041-s	20	25	22.5
57081-s	15	21	18.0
58564-s	10	22	16.0
58572-s	10	26	18.0
59009-s	8	15	11.5
59010-s	14	15	14.5
59011-s	8	24	16.0
59012 s	10	15	12.5
59013-s	9	25	17.0
59100-s	20	21	20.5
70957	13	10	11.5
70960	14	23	18.5
71070	13	20	16.5

[1] Difference required for significance = 8.8

cultural study. The comparative growth rates are shown in fig. 3. These growth rates were compared by the analysis of variance method, and the data are presented in tables 8 to 12 inclusive. Plates 6 and 7 illustrate the growth of some of these isolates on string bean agar.

When the differences required for significance in these tables are compared with the differences in average growth of the various isolates, it is apparent that again the time-growth curve discloses considerable variation. The results are comparable to those discussed previously in tables 3-6 inclusive. At the end of the 12-day interval many of the differences found to exist between isolates at the end of 3-, 6-, and 9-day intervals, have disappeared. The F value for the isolates in table 12 shows that the differences observed are highly significant. The relatively large value be-

TABLE 10

Analysis of Variance of Radial Growth in Millimeters After 9 Days Incubation of 28 Isolates of F. fomentarius on 2 Media

Isolate	Radial growth in millimeters at 9 days on		Average[1]
	Malt agar	String bean agar	
F 1	26	37	31.5
F 4	24	15	19.5
F 6	23	36	29.5
F 9	25	37	31.0
F 10	26	35	30.5
F 102	32	32	32.0
F 103	35	29	32.0
F 105	7	11	9.0
F 111	10	15	12.5
F 196	30	30	30.0
F 197	30	32	31.0
F 206	32	37	34.5
F 1307	17	25	21.0
F 2252	25	15	20.0
F 3309	3	6	4.5
17041-s	35	43	39.0
57081-s	28	43	35.5
58564-s	32	40	36.0
58572-s	29	42	35.5
59009-s	25	35	30.0
59010-s	34	38	36.0
59011-s	16	33	24.5
59012-s	24	40	32.0
59013-s	26	43	34.5
59100-s	40	42	41.0
70957	26	37	31.5
70960	25	40	32.5
71070	27	35	31.0

[1] Difference required for significance = 9.9

tween the 3-day growth intervals corroborates the previous conclusion that the time-growth factor introduces considerable variation in the relative growth rates. Macdonald (*52*) worked with 11 isolates of *F. fomentarius* including F 102, F 103, F 105, and F 111. He concluded that there was considerable variation in the rate of growth, rate of development of color, and intensity of color on the different media.

It was impossible to find similarity when grouping these 28 isolates on the basis of either host or locality from which the isolate originated. There was almost as much variation within the isolates from a given host as there was when the isolates from different hosts were compared. Plate 8 shows 5 isolates from white birch and 1 from an unknown species of birch. There is more variation between these isolates than in the isolates shown in

TABLE 11

Analysis of Variance of Radial Growth in Millimeters After 12 Days Incubation of 28 Isolates of F. fomentarius on 2 Media

Isolate	Radial growth in millimeters at 12 days on		Average[1]
	Malt agar	String bean agar	
F 1	40	40	40.0
F 4	45	34	44.5
F 6	37	43	40.0
F 9	40	43	41.5
F 10	32	40	36.0
F 102	45	44	44.5
F 103	40	45	42.5
F 105	10	14	12.0
F 111	15	25	20.0
F 196	42	45	43.5
F 197	45	45	45.0
F 206	45	45	45.0
F 1307	20	31	25.5
F 2252	38	25	31.5
F 3309	9	12	10.5
17041-s	47	47	47.0
57081-s	45	45	45.0
58564-s	45	43	44.0
58572-s	42	45	43.5
59009-s	43	43	43.0
59010-s	45	45	45.0
59011-s	20	44	32.0
59012-s	42	42	42.0
59013-s	45	48	46.5
59100-s	45	45	45.0
70957	42	43	42.5
70960	35	47	41.0
71070	39	40	39.5

[1] Difference required for significance = 9.2

TABLE 12

Analysis of Variance of Radial Growth in Millimeters of 28 Isolates of F. fomentarius on 2 Media

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	223	54285.2		
Between isolates	27	6808.5	252.1	7.3
Between 3-day growth intervals	3	40166.4	13388.8	39.0
Between media	1	714.3	714.3	20.8
Error	192	6596.0	34.3	

Plate 9, where isolates from three different hosts are compared, or in Plate 10, where isolates from 6 hosts are compared.

The present study seems to confirm the results of several other investigators, such as Mounce (*54*), Percival (*62*), and Herrick

(*38*), all of whom found that various isolates of the same fungus varied widely in growth rate as well as in the character and color of the mycelium. The 28 isolates of *F. fomentarius* in the present study exhibit considerable variation which is independent of either host or locality influence and is apparently the result of individual variation. The cultural characters observed, while differing widely in some instances, nevertheless do not fall outside the range of characters given by Rumbold (*76*), Fritz (*33*), and Campbell (*17*). Campbell gives a complete description, based on isolate 17041-s, of the cultural characteristics of *F. fomentarius*. None of the variations observed in the 28 isolates studied warrant any changes in this description.

All the isolates were grown on tannic and gallic acid media. Davidson, Campbell, and Blaisdell (*25*) cultured 12 isolates of *F. fomentarius* on these two media and obtained the oxidase reaction. Macdonald (*52*) also obtained the oxidase reaction with 11 isolates of this fungus. Similarly all 28 isolates of *F. fomentarius* studied here gave this reaction. It was impossible to find any definite variation in the intensity of the oxidase reaction.

ACIDITY

The pH of malt agar was adjusted colorimetrically at different concentrations following the procedure outlined by Rawlins (*70, pp. 71-73*). Isolates from 5 hosts were grown on this agar for 10 days at 22° C. in a constant-temperature chamber. The cultures were grown in petri dishes in duplicate. A comparison

TABLE 13

Mycelial Growth of Fomes fomentarius After 10 Days on Malt Agar of Different pH Concentrations

Culture #	pH 3.8–4.2	pH 4.8–5.2	pH 5.8–6.2	pH 6.8–7.2	pH 7.8–8.2
F 1	23[1]	36	44	48	31
F 6	28	30	45	46	26
F 10	30	39	42	49	26
58564-s	36	42	46	48	38
59010-s	28	39	43	48	30
59011-s	29	40	42	43	20
59012-s	22	31	45	47	35

[1] Each measurement is the average radial growth in two petri dishes.

was also made between one of the preceding isolates, which was from white birch, and two other isolates from the same host. The radial growth in millimeters was measured at the end of the 10-day interval. The data are presented in table 13. It is apparent that *Fomes fomentarius* is not markedly influenced by differences in pH within the range tested. The optimum pH appears to be approximately 7. Isolates from different hosts, and isolates from the same host as found in different localities, grow well over a wide range of pH with no specific differences between the isolates.

TEMPERATURE

Isolates from various hosts were grown on malt agar at different temperatures. Cultures were incubated for 10 days at 0° C., 15° C., 20° C., 25° C., 30° C., and 35°C., in constant-temperature chambers in darkness. Cultures were grown in duplicate, in petri dishes, on malt agar, at a pH of approximately 6.8, and the radial growth in millimeters measured at the end of the 10-day interval. The data are presented in table 14. From this table it is evident that various isolates may show only minor differences in regard to the relationship of temperature to growth. The optimum temperature is between 25° C. and 30° C., the minimum apparently just below 15° C., and the maximum somewhat above 35° C. Again it was impossible to find any similarity between the isolates from a given locality or a given host, in their response to temperature.

Experiments proved that the thermal death point of the hyphae of *F. fomentarius* was approximately 45° C. The time of

TABLE 14

Mycelial Growth of Fomes fomentarius After 10 Days on Malt Agar at Various Temperatures

Culture #	0° C.	15° C.	20° C.	25° C.	30° C.	35° C.
F 1	0[1]	4	30	50	46	18
F 4	0	2	32	48	42	12
59100-s	0	2	32	44	50	16
59010-s	0	4	26	42	48	18
70960	0	4	32	46	50	16
58564-s	0	4	30	44	50	16

[1] Each measurement is the average radial growth in two petri dishes.

heating had no apparent effect. Heating for 8 minutes gave similar results to heating for 1, 3, 5, 10, 20, or 30 minutes.

CONCLUSION ON GENERAL CULTURAL STUDIES

As a result of these general cultural studies it seems that strains do not exist in *F. fomentarius*. When isolates from different hosts or localities are grown on artificial media, more variation in growth rate is caused by the medium than by the source of the isolate. This variation is associated with the time-growth factors of the various isolates, and it is probable that if cultural studies could be conducted over a sufficiently long period of time, the differences in rate of growth between isolates would disappear, or at least not be statistically significant. No differences were found between isolates in their response to acidity, temperature, or the ability to cause the oxidase reaction on gallic or tannic acid media.

AVERSION BETWEEN DIPLOID CULTURES

An extensive literature has appeared during recent years on the antagonism that occurs between fungi in mixed cultures. It has long been known that when two cultures are grown together in the same petri dishes or agar slant the hyphae of the two colonies may not intermingle and may form a definite line which sometimes is heavily pigmented. Various terms have been used to describe this phenomenon. Arnold (*3*) listed: "line of demarkation," "inhibition," "aversion," "repulsion," "barrage," and "Hemmungsreaktion." Line of demarkation seems to be the most commonly used term in describing this phenomenon among wood-rotting fungi. Porter (*63*) has described 5 types of reaction when two fungi are grown together: (1) two organisms intermingle mutually, (2) one organism overgrows and inhibits the other, (3) both organisms inhibit each other slightly, (4) one organism grows around the other, and (5) both organisms inhibit each other distinctly.

The occurrence of some or all of these types has been recorded by many investigators. Brown (*12*), and in several other

papers, and Pratt (*65, 66*), as well as many other investigators, have recorded this phenomenon when two different genera, such as *Botrytis* and *Fusarium,* were grown together on synthetic media. The formation of a line of demarkation has been frequently described as occurring between diploid isolates of the same species. Mounce (*54*), for example, found with *Fomes pinicola* that complete intermingling occurred only: (1) when a mycelium is paired with itself, (2) when mycelium from sporophore tissue is grown with mycelium from spores produced by the sporophore, (3) usually when mycelium from infected wood of a tree is grown with mycelium from a sporophore which grew upon the tree, and (4) usually when mycelium from spores or sporophore tissue is grown with mycelium from spores or sporophore tissue from a second sporophore from the same tree. Verrall (*86*) working with *Fomes igniarius* made tissue isolates from fruiting bodies growing respectively at heights of 2, 5, 7, 10, 15, and 20 feet on a quaking aspen tree. The isolate from the sporophore growing at 2 feet formed a line of demarkation when plated against all other isolates except itself. All the other isolates were mutually compatible. This isolate was different from all the others in appearance in culture, and an examination of the wood in the tree showed that this isolate probably represented a different infection and thus two distinct mycelia were in the tree. A line of demarkation has been recorded between monosporous isolates of one species. For example, Schmidt (*78*) recorded it in certain species of the Phycomycetes, Cayley (*22*) in certain species of the Ascomycetes, and Vandendries (*83*) in certain species of Basidiomycetes.

The cause of demarkation has been ascribed to many different factors. Brown (*13*) attributed it to staling as caused by the production of ammonia and carbon dioxide. The medium absorbed the ammonia and became alkaline, and a line of demarkation resulted. Pratt (*65*) attributed staling and a line of demarkation to the deposition of salts of organic acids. Later, Pratt (*66*) stated that staling was caused by the formation of bicarbonates from the carbon dioxide of respiration. A good review of the literature on staling is given by Porter and Carter (*64*).

Mutual antagonism between fungi has been attributed to the formation of toxins as by-products of metabolism. Porter and Carter (*64*) and D'Aeth (*1*) reviewed the literature on metabolic

by-products. Gioelli (*35*) attributed mutual antagonism between species of *Penicillium* to the formation by both organisms of certain toxins which were thermostable and capable of ultrafiltration. Carter (*21*),Arrillaga (*4*), Blattny (*8*), and Alexopolus, Arnett, and McIntosh (*2*) all found toxic substances which were soluble, diffused into agar, and frequently survived autoclaving. Carter (*21*) found that he could cut a strip of agar from one colony and produce aversion by placing the agar strip in the path of a growth of a different colony. Mounce (*54*) found with *F. pinicola* that the hyphae would grow over such a strip of agar and form a line of demarkation only when the two advancing hyphae met. Arrillaga (*4*) found that the formation of a line of demarkation was independent of pH changes and that the toxin produced was not an enzyme as it could be heated to 110° C. Fleming (*31*) isolated a definite substance, produced by a species of *Penicillium,* which was rather unstable and appeared to be non-enzymatic. Reid (*71, 72*) found a toxic substance that was relatively thermostable, but exposure to light, or gaseous oxygen, hydrogen, and carbon dioxide prevented its formation or caused its destruction. Kent (*46*) found a toxic substance, produced by *Diplodia zeae,* that was not destroyed by oxidation, by correction of the pH, by replacement of sugars in the cultural medium, by moderate hydrolysis under alkaline or acid conditions, or by boiling for 1 hour. The toxin was also alkaline in reaction and insoluble in ether.

Other investigators have simply stated that "physiological differences" caused a line of demarkation. Hoppe (*43*) studied *Diplodia zeae* and concluded that a line of demarkation was caused by strains that were physiologically different. He made single-spore isolations and found that the property of aversion remained stable through 3 generations and also through passage through corn. Schmitz (*79*) and Mounce (*54*) both worked with *Fomes pinicola* and concluded that the isolates they used were physologically different.

The inheritance of the capacity of forming a line of demarkation has been studied by many investigators. For example, Cayley (*22*) found that the formation of a line of demarkation was inherited and segregated along Mendelian lines. Vandendries (*83*) and Kaufert (*45*) found that it was dependent upon certain combinations of Mendelian factors and could be traced to a distinct

correlation between the occurrence of this and the common possession of the a or a′ factors by the paired mycelia. Verrall (*86*) stated that "through segregation and recombination almost every mycelium is genetically different with respect to the factor or factors influencing compatibility."

The formation of a line of demarkation occurred when any two of the 28 isolates of *Fomes fomentarius* listed in table 2 were grown together in the same petri dish or agar slant. Complete intermingling occurred only when an isolate was plated with itself. Practically all the types of reactions in mixed cultures described by Porter (*63*) and Mounce (*54*) were found to exist in *F. fomentarius*. Plate 11, E, and Plate 12, E, show mutual intermingling when the same isolate is plated with itself. Plate 12, A, shows mutual inhibition in which a sterile strip of agar occurs between the two colonies. Unlike the type described by Verrall (*86*) there was no intermingling of submerged hyphae. Plate 12, B, shows mutual inhibition in which the hyphae actually touch. Plate 12, F, shows a slight inhibition of one colony by the other, and Plate 11, D, shows one organism inhibiting and almost completely growing around the other. When isolate 58572-s was plated against F 105, which is a slowly growing isolate, the aerial hyphae of 58572-s would surround and overgrow the colony of F 105. A definite line of demarkation occurred where the hyphae met in the medium. The same was true when F 206 was plated against F 102, F 103, F 105, F 197, and F 1307.

In order to determine whether a toxin which would cause a line of demarkation was present, a series of pertinent experiments were planned. Following the method described by Mounce (*54*), isolates 57081-s and 59011-s (see Plate 12, B) were grown in a petri dish on malt agar. When the colonies were about 10 millimeters in diameter a strip consisting of some clear agar and a small amount of mycelium was removed from the margin of each colony. These strips were interchanged, placing the clear agar part toward the advancing hyphae of the other colony. If the line of demarkation is caused by metabolic by-products that are diffusable into the agar the line should form where the mycelium of 57081-s met the agar strip from 59011-s and *vice versa*. This, however, did not happen, as the line formed only when the hyphae of the two colonies actually met. In a similar experiment when 59013-s and F 1

were used (see Plate 12, A), a line of demarkation did form before the hyphae actually touched, and a sterile strip of agar remained between the two colonies This, however, was the exception, and usually the hyphae touched before a line of demarkation was formed.

All attempts failed to isolate a toxin from the substratum upon which an isolate of *F. fomentarius* had been grown. Various isolates were grown on liquid 2.5 per cent malt extract, in Kolle culture flasks, until a large pad of mycelium was formed. This pad was then macerated under sterile conditions and allowed to stand for 24 hours. The clear liquid was then decanted and centrifuged and the centrifuged extract passed through a Seitz filter. However, when this was replated together with another isolate, this isolate grew over the liquid and did not form a line of demarkation (see Plate 13,B). Further experiments, varying the time the macerated mass was allowed to stand under sterile conditions before centrifuging and filtering, gave identical results.

Since the process of filtration might have removed a toxin, the experiment was repeated, and, after centrifuging the liquid was heated to various temperatures. It was found that heating at 35° C., 40° C., and 45° C. permitted fragments of hyphae to survive and give rise to numerous colonies when replated. Heating above 45° C., however, permitted the isolate to grow over the entire petri dish.

Brown (*13*) found staling to be associated with the production of a volatile gas. Therefore, various isolates of *F. fomentarius* were grown in separate petri dishes and after the colonies had reached a diameter of approximately 10 millimeters the tops of the dishes were removed and the two bottoms placed together. The resulting dish was sealed with sterile tape. Both isolates continued growth until the medium was covered with hyphae, with no toxic effects apparent. As there still remained the possibility that a gas could be formed in small quantites and leak out through the sterile tape, the experiment was repeated and the petri dishes consisting of the bottoms of two dishes each containing a different isolate were incubated under a mercury seal. However, the results were similar to those previously described.

As several investigators had stated that physiological differences existed, an attempt was made to measure any such possible differences in the isolates of *F. fomentarius*. Two isolates were

grown in the same petri dish, using a combination like that shown in Plate 11 C, where a strip of sterile agar occurs between the two colonies, and expands at its junction with the wall of the petri dish. Samples of approximately 5 square millimeters were then removed from beneath each colony, from either side of a colony, and from the sterile strip between them. These samples were then macerated under sterile conditions in sterile water and allowed to stand for 24 hours. There were no measurable differences between any two of the 5 samples in the pH as measured electrometrically, in the oxidation-reduction potential, in the specific conductivity, or in the osmotic pressure as determined by the depression of the freezing point.

Although all attempts to learn the cause or causes of this line of demarkation failed, it is still possible that a toxin was formed, or that physiological differences existed, and that neither of these could be demonstrated with the technics employed here. Most of the previous investigations on the line of demarkation, which happen to be centered on the inheritance of this phenomenon, have described the formation of the line following the actual touching of the hyphae in the two advancing colonies. However, in several of the combinations studied with the isolates of *F. fomentarius,* a sterile strip of agar occurred between the two colonies (see Plate 12 A, D, and F). The possibility of the inheritance of the capacity to form a line of demarkation was not studied in *F. fomentarius.*

CULTURE STUDIES ON WOOD

In order to study the relative saprogenicity of these various isolates a series of inoculations were made on wood blocks. Following the method described by Percival (*62*), 20 wood blocks of the sapwood and 20 of the heartwood of yellow birch were inoculated with isolate F 6. The wood blocks were 1-inch cubes varying from 10.4 to 11.2 grams in weight. After being weighed, they were boiled in water until they sank, and were placed in beakers as follows: Small pieces of glass tubing were placed in the bottom of each beaker. A layer of absorbent cotton was placed over the top of this tubing, and a small amount of water added to each beaker. Ten of the 1-inch cubes were then placed in each of the beakers. These cubes were arranged in 3 layers, 4 cubes in the lowest layer

and 3 in each of the others, with a triangular space in the middle of each 3-cube layer, in which the inoculum was to be placed. Each beaker was covered with a layer of cotton and a petri dish cover, after which it was autoclaved at 15 pounds pressure for 20 minutes. The cubes were inoculated and stored for 8 months. Sterile water was added at the end of 3 months and again at the end of 6 months. At the end of 8 months the beakers were opened and the mycelium removed from the wood blocks. These were then stored in the laboratory during the winter until they reached a constant weight. The mean loss with its probable error for the heartwood blocks was 5.33 ± .325 per cent (from an original mean weight of 10.05) and for the sapwood blocks 6.28 ± .573 per cent (from an original mean weight of 10.23). The difference between these two means with its probable error is .95 ± .657 per cent. This difference is only slightly greater than its probable error, so the odds that it is significant are only slightly greater than 1:1, which is not significant.

A second series of wood inoculations was performed in 1-quart glass Mason jars. Here wood sticks, ½ x ½ x 6 inches, were used, following the method described by Owens (*61*). Wet paper toweling was placed in the bottom of the jars, and 50 cc. of a 2.5 per cent malt extract was added to each jar. Then 5 wood sticks were weighed and placed on end in each jar. A thin layer of cotton was placed over the top of each jar and the glass cover clamped down. The jars were then autoclaved for 15 minutes at 20 pounds pressure. A large portion of inoculum was placed on the malt-extract-soaked paper toweling, and the jars were stored for 11 months (see Plate 14). The jars were then opened, the mycelium was removed from each wood stick, and the sticks were stored in the dry laboratory during the winter until they reached a constant weight. The losses in weight were tabulated. The resulting data were compared by the analysis of variance method, and the results are presented in tables 15 and 16.

Table 15 shows the results when 3 isolates from Maine were inoculated onto their 3 native hosts in all possible combinations. If host influence had a measurable effect on the rate of wood decay it seems probable that an isolate from yellow birch would produce more decay in that wood than in either gray or white birch. However, F 6, an isolate from yellow birch, and F 10, an isolate from

white birch, do not differ significantly. F 1, an isolate from gray birch, is significantly different from both F 6 and F 10. When the woods are compared by calculating the difference required for significance, significant differences exist only when the white birch wood is compared with the yellow birch.

TABLE 15

Analysis of Variance of Loss in Weight in Grams of Wood Sticks Incubated for 11 Months with 3 Isolates of F. fomentarius

Isolate from	Wood						Average[1]
	Yellow birch		Gray birch		White birch		
	Loss in wt. gms.		Loss in wt. gms.		Loss in wt. gms.		gms.
Yellow birch F 6	13.2	10.6	10.0	12.8	20.2	21.2	14.69
Gray birch F 1	17.8	10.5	17.1	14.8	15.2	33.3	18.11
White birch F 10	9.3	7.1	15.6	11.1	16.9	13.2	12.20
Average[2]	13.43	9.40	14.23	12.90	17.43	22.60	
	11.41		13.56		20.01		

[1] Difference required for significance = 6.6
[2] Difference required for significance = 6.6

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	17	757.96		
Between isolates	2	105.92	52.96	1.7
Between woods	2	240.37	120.18	3.8
Between jars	1	0.20	0.20	0.0
Interactions				
Isolates—woods	4	27.27	6.82	0.2
Isolates—jars	2	30.15	15.08	0.5
Woods —jars	2	227.10	113.55	3.6
Error	4	126.95	31.74	

When the F values are calculated, however, it is found that no significant differences occur. The F value for cultures is 1.7 and that for woods is 3.8. Neither is significant at the 5 per cent point. Therefore it may be concluded that significant differences do not occur, as the chances that the differences observed are due to chance are greater than 5 in 100.

Table 16 shows the results when 9 isolates of *F. fomentarius* from various hosts are inoculated onto yellow birch wood. Here it is shown that F 1 differs significantly only from F 3309, an English isolate from white ash.

F 10 differs significantly only from F 1307, a Canadian isolate from beech.

F 6 differs significantly from F 1307 and F 3309.

70960, an isolate from yellow birch in Wisconsin, differs significantly only from F 3309.

F 1307 differs significantly from all isolates except F 1 and 70957, the latter an isolate from maple.

F 4 differs significantly from F 1307 and F 3309.

F 3309 differs significantly from all isolates except F 10.

59009-s, an isolate from poplar, differs significantly only from F 3309.

70957, an isolate from maple, differs significantly from F 1307 and F 3309.

In all these differences F 1307 caused the greatest amount of decay, and F 3309 the least amount.

TABLE 16

Analysis of Variance of Loss in Weight in Grams of Yellow Birch Wood Sticks Incubated for 11 Months with 9 Isolates of F. fomentarius

Isolate from	Loss in weight		Average[1]
	gms.	gms.	gms.
Gray birch F 1	17.8	10.5	14.15
White birch F 10	9.3	7.1	8.20
Yellow birch F 6	13.2	10.6	11.90
Yellow birch 70960	11.9	16.5	14.20
Beech F 1307	34.5	18.2	21.3
Elm F 4	11.2	10.4	10.80
White ash F 3309	0.9	1.3	1.10
Aspen 59009-s	10.3	8.8	9.55
Maple 70957	15.1	12.9	14.00

[1] Difference required for significance = 7.9

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	17	909.99		
Between isolates	8	730.18	91.27	5.8
Between jars	1	54.37	54.37	3.4
Error	8	125.44	15.68	

The F value for jars is 3.4, which is not significant at the 5 per cent point.

The F value for isolates is 5.8, which is significant at the 5 per cent point but not at the 1 per cent. Therefore it is apparent that significant differences between various isolates occur in their relative ability to cause decay of wood, and that these differences are not the result of host influence, but rather of individual variation.

The isolates of this fungus differ in their ability to cause decay of wood, but these differences are the result of individual variation, and are not correlated with any host or locality influence. For example, an isolate from yellow birch will not decay the wood of yellow birch to any greater extent than it will the wood of either white or gray birch. An isolate from beech, however, may decay yellow birch to a much greater extent than isolates from yellow birch.

NATURAL DECAY

Fomes fomentarius causes a white mottled rot of the sapwood and heartwood of many hardwoods, principally birch, beech, and poplar. This is one of the most common rots of hardwoods in the Northeast, and in forests of the northern hardwood type, probably does its greatest damage to over-mature trees. Drayton (*26*) recorded data on 25 birch trees that were selected, felled, and examined for wood rots on a representative area in eastern Canada. All the trees were over-mature, from a silvicultural standpoint, and were badly decayed. *F. fomentarius* had decayed 71 per cent of the trees and *F. igniarius* 8 per cent, while 21 per cent had been decayed by both fungi. The occurrence of *F. fomentarius* in old beech stands has been recorded by Felt and Rankin (*30, p. 162*), Ulbrich (*82*), and Frölich (*34*). Vanin (*84*) observed that pure plantations of birch in Russia were found to be more heavily infected with *F. fomentarius* and *Polyporus betulinus* than mixed stands were.

According to Baxter (*5*), *F. fomentarius* in Europe is considered to be a "strong" parasite while in the United States it is not so regarded. Biers (*6*) noted the parasitic nature of this fungus on poplar trees in France. Borissoff (*9*) stated that *F. fomentarius* is the chief local parasite on *Juglans regia* in the Caucasus. Lowag (*50*) recorded the production of pronounced ridges in the sapwood

of European beech in Germany as caused by the parasitic nature of this fungus. Rozanova (*75*) found *F. fomentarius,* in the Zvanigorod district in the government of Moscow in Russia, living much more as a saprophyte than as a parasite. This was in direct contradiction to previous observations in the government of Smolensk where the organism was equally parasitic and saprophytic. She suggested that this discrepancy might be due to the fact that in the government of Smolensk birches usually grow in a mixed forest of spruce and hardwoods and therefore are lower in vitality.

The parasitic nature of *F. fomentarius* in the sapwood of many hardwoods has been recorded by numerous other investigators. Freeman (*32, p. 251*) considered the fungus to be a dangerous parasite, as when it gains entrance through the stem it grows chiefly upward and downward from the point of entrance and kills the sapwood. Von Schrenk and Spaulding (*80*), Rankin (*69, p. 105*), Hubert (*44, p. 379*), and Felt and Rankin (*30, p. 170*) all stated that the fungus entered the tree through the sapwood, next to the bark, and had a girdling effect on the tree. Sorauer (*81, p. 382*) illustrated the rot of this fungus as a sapwood rot in a beech stem. Neger (*58*) considered the fungus to be parasitic on beech, hornbeam, and elm, and rarely parasitic on birch, alder and horse chestnut.

Faull (*28, 29*) pointed out that if *F. fomentarius* were a sapwood rot, the fungus would differ in habit from all other polypores. He stated that the true relationship of the organism is that it gains entrance through wounds, such as dead branch stubs in the crown, and the mycelium passes through dead or inactive tissue until it reaches the heartwood. Then it progresses vertically, both up and down, in the tree. At the same time, adjacent lateral cells are being weakened and invaded and the fungus advances into the sapwood until the cambium is reached and killed. Eventually enough cambium is killed so that the crown dies. Faull also noted the work of Rostrup (*74, pp. 371-376*) as being the first true account of the heartwood-rotting nature of this organism. Weir (*87*) observed that *F. fomentarius* caused a heartwood rot of apple, and Prutensky (*68*) noted that this fungus caused a heartwood rot of walnut. Lowag (*50*) described how the mycelium of this organism grows in the heartwood of beech in Austria and how the decay finally reaches the sapwood and kills the cambium.

Sporophores of *F. fomentarius* are rare on living trees in

Maine, but finally they were found on two such trees. One of these trees was a white birch at Sieur De Monts Spring, Acadia National Park, Mt. Desert Island.[3] The other tree was a yellow birch tree on Black Cap Mountain near Eddington. These two trees were cut down and examined. The trunks and branches were cut into 4-foot bolts and then these were split lengthwise. The rot was traced in each bolt and samples taken for culturing.

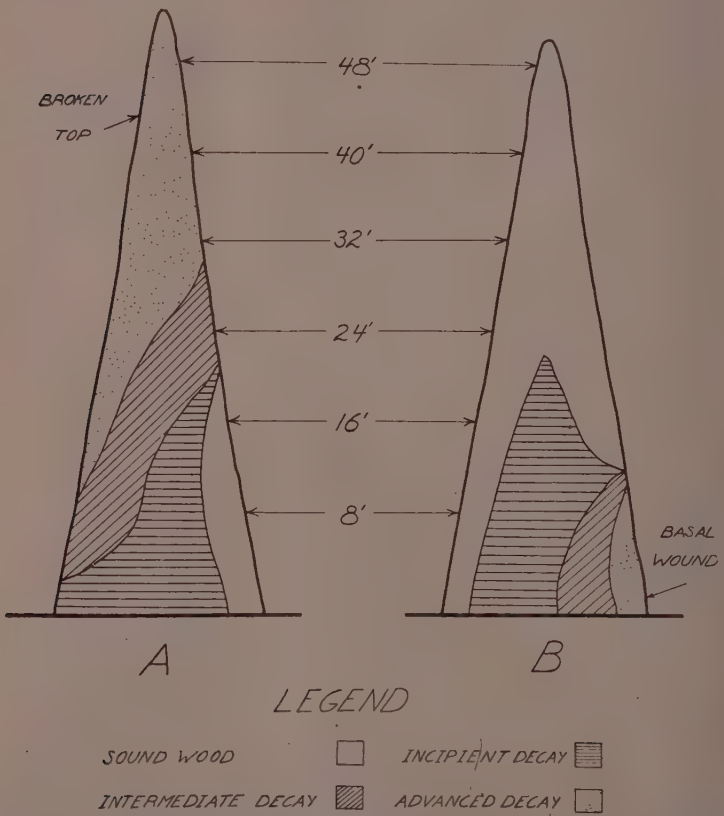

FIG. 4. Diagram of the extent of rot produced by *Fomes fomentarius* in (A) yellow birch and (B) white birch.

[3] Thanks are due Mr. B. Hadley, Supt. of Acadia National Park, for permission to cut down this white birch tree.

Cultures typical of *F. fomentarius* were isolated from the decayed wood. The distribution of the rot in each of these trees is shown diagrammatically in fig. 4. In the yellow birch tree it is apparent that the fungus entered the upper end of the bole through a dead branch or a branch stub, and spread down the trunk through the heartwood, and attacked the adjacent sapwood. In the white birch tree, the fungus entered through a wound at the base of the trunk, and then went up the trunk in much the same manner. The distribution of the rot in each of the 4-foot bolts of the white birch tree is shown in Plate 15. The first 4-foot bolt in Plate 15 shows that the fungus is capable of attacking heartwood and dead sapwood simultaneously. In the second 4-foot bolt, however, a narrow band of healthy sapwood appears, which increases in size until the 20-foot bolt is reached and there the fungus is restricted to the heartwood.

Boyce (*10, pp. 12-15*) has discussed the confusion in forest pathological literature that results from the use of the terms "parasite" and "saprophyte" as applied to wood-rotting fungi. *F. fomentarius* has been called a parasite by most European workers, and a saprophyte by most American ones. It is apparent that *F. fomentarius* is capable of attacking both "living" and "dead" cells. It may, therefore, be considered both parasitic and saprophytic with respect to parts of the tree, and parasitic with respect to the tree as a whole. In all cases it causes a decay and is, therefore, saprogenic. Therefore the term "saprogen" proposed by Ehrlich (*27*) seems most applicable here.

Macroscopical Characters

In the incipient stage of decay, the wood is brownish, with no other apparent alteration. In the intermediate stage, the wood in radial view has a mottled appearance caused by the streaks or irregular patches of white or yellowish mycelium and also by the decay. In the advanced stage, the wood is yellowish white, soft and spongy, and is characterized by narrow, dark bands running through it. In a typical block of decayed wood, these may appear as black flecks of irregular shape (see Plate 16, block on extreme right). These bands are usually masses of brownish, swollen hyphae in the wood rays. Mycelial pads in the cracks of the infected wood are common.

It is interesting to note the similarity of the incipient decay caused by *F. fomentarius* to the so-called "red-heart" of birch that occurs throughout the commercial white birch stands of Maine. This red-heart of birch, which is actually brownish in color, is probably the most serious disease of birch trees in Maine. The disease is more common in birch stands that are being grown on poor sites, particularly on thin soil or in swamps. The birch stands of southwestern Maine, where this disease is most common, are all composed of second-growth trees, with sprout or seedling-sprout trees predominating. Here red-heart usually occurs in the first 4- to 8-foot bolt, but sometimes occurs as high as 32 feet up the tree. Red-hearted wood is discriminated against at the mill, and thus the existence of this disease in a large part of a birch stand may mean that cutting operations will be conducted at a financial loss to the operator.

Unfortunately, cultural studies on the fungi isolated from red-hearted birch trees have been inconclusive. Field inoculations of *F. fomentarius* have been started in Maine, but a long period of years may be required before any data can be obtained.

MICROSCOPICAL CHARACTERS

Histological sections of infected wood were prepared in order to study the microscopical features of decay. Sections of white birch were typical of the decay described as caused by *F. fomentarius*. Hyphae were most abundant in the wood rays and the lumina of the vessels. In the wood rays the hyphae frequently become swollen and filled with dense-staining, somewhat granular masses, and thereby become much like the bladder cells described as occurring in the black zone lines associated with some kinds of decay. The cell walls of the wood ray cells in badly decayed wood are characterized by enlarged pits and numerous bore holes. The hyphae apparently do not necessarily take the easiest way in which to go from cell to cell. Frequently a hypha could be traced, which had not only penetrated a simple pit in a wood ray cell, but then had penetrated the cell wall of another wood ray cell just to one side of a pit, where it formed the hour-glass shaped bore hole described by Hubert (*44, pp. 89, 379*) and Macdonald (*52*). Bore holes were also observed in the tori of bordered pits in the fibers.

One of the most common features observed in the sections of decayed wood was the occurrence of masses of hyphae in the lumina of the vessels. Frequently the vessels would be completely filled with these closely-packed masses of hyphae.

In cross section, the effect of the hyphae on the secondary cell walls of fibers is conspicuous. As is shown in Plate 17,[4] the secondary walls are readily attacked. In the center of the wood section shown in Plate 17, the secondary cell walls of the fiber cells are almost entirely gone, while elsewhere the secondary cell wall sometimes appears almost normal in thickness.

CHEMICAL COMPOSITION

Inasmuch as white birch is the most common host of *Fomes fomentarius* in the northeastern part of the United States, wood of this species was selected for use in determining the effect of decay upon chemical composition. One-inch cubes were inoculated with culture F 10, and incubated for 8 months, in the manner previously described. These wood cubes were then separated into three groups on the basis of their loss in specific gravity. These groups were ground up separately until they would pass a 60-mesh sieve. Selected screens were not used, because of the errors (such as selective effect on materials of different composition) that Scheffer has pointed out as being likely to result from their use. The samples were placed in airtight containers, and moisture determinations were made on duplicate samples, thus avoiding the oven-drying of the samples to be tested. The methods of analysis were those selected and described by Bray (*11*).

The data are presented in table 17. Cellulose was attacked much more than lignin, and apparently the greater proportion of the cellulose depletion occurred in the early stages of the decay. A cellulose depletion by other white rots has been recorded by Hawley and Wise (*37*), Hirt (*41*), Campbell (*20*), Hirt (*42*), and Scheffer (*77*). It is obvious that although *Fomes fomentarius* depletes the lignin somewhat in white birch wood, the fungus is not a lignin-preferring species.

It is also obvious that there was no differentiation in the utilization of the pentosans. The pentosans in cellulose were depleted

[4] Photomicrograph by ultraviolet light made by Dr. P. Proctor.

TABLE 17

Effect of Decay on the Chemical Composition of White Birch Wood[1]

Kind of component	Amount of component expressed as percentage of wood samples at different relative specific gravities					
	With percentage based upon samples analyzed			With percentage based upon original weight of dry sound wood		
	Relative sp. gr. 100[2]	Relative sp. gr. 60	Relative sp. gr. 40	Relative sp. gr. 100	Relative sp. gr. 60	Relative sp. gr. 40
	Per cent	Per cent	Per cent	Per cent	Per cent	Per cent
Cold water soluble	2.1	3.7	7.3	2.1	2.2	2.9
Hot water soluble	2.3	5.1	9.1	2.3	3.1	3.6
Strictly hot water soluble	0.2	1.4	1.8	0.2	0.8	0.7
Alcohol-benzene soluble	2.5	2.4	2.3	2.5	1.4	0.9
Total 1% alkali soluble	17.4	26.4	31.0	17.4	15.8	12.4
Strictly 1% alkali soluble	15.1	21.3	21.9	15.1	12.8	8.8
Cellulose	59.5	53.9	54.9	59.5	32.3	22.0
Lignin	21.3	22.9	19.0	21.3	13.7	7.6
Total pentosans	25.7	25.9	24.8	25.7	15.5	10.0
Pentosans in cellulose (cellulose basis)	22.0	23.7	20.9	22.0	23.7	20.9
Pentosans in cellulose (wood basis)	13.1	12.8	11.5	13.1	7.7	4.6
Pentosans not in cellulose	12.6	13.1	13.3	12.6	7.9	5.3

[1] All these analyses were made by Mr. C. W. Ziemer.

[2] "Relative specific gravity" here means the percentage that the specific gravity of the decayed wood is of the specific gravity of sound wood. Thus the sound wood, with a specific gravity in this case of about .60, is considered to have a relative specific gravity of 100, and decayed wood here with a specific gravity of .36 would have a relative specific gravity of 60. The decrease in relative specific gravity is a measure of the amount of decay.

in the same proportion as those not in cellulose. This is in contrast to the preferential selection of the pentosans in cellulose reported, according to Scheffer (*77, p. 39*), to be characteristic of the brown rots. Also in contrast, Campbell (*20*) found that *Fomes fomentarius* acting on beech wood, attacked the pentosans in cellulose to a greater degree than those not in cellulose. Scheffer (*77*) found that *Polyporus versicolor* (a white rot) utilized the pentosans not in cellulose first and that shortly afterward the pentosans in cellulose were attacked.

The fact that there is a decrease in alkali solubility as shown in table 17, is in agreement with the findings of Campbell (*20*) and Scheffer (*77*) on this rot and other white rots. Further, Campbell (*18, 19*) has shown that one of the principal chemical bases of differentiation between the white and brown rots is the alkali solubility of the decayed wood. In brown rots the increase in alkali solubility is roughly proportional to the cellulose depletion, while in white rots there is no correlation between alkali solubility and the loss of any other chemical component. The results here are again in agreement.

CALORIFIC VALUE

Determinations of the calorific value of decayed wood have been used by several investigators to evaluate the rate of such decay. Lehmann and Scheible (*47*) investigated the loss in calorific value of pine sawdust inoculated with various fungi. A maximum loss of 42.9 per cent was recorded for the sawdust after an incubation period of 6 months with *Armillaria mellea* (Vahl.) *Quél.* Other fungi gave lower readings. *Daedalea quercina* (L.) Fr. caused a loss of only 8.1 per cent. Vanin and Esupoff (*85*) also investigated the effect of decay on calorific value, presenting data showing losses from 21.4 to 72.3 per cent. Scheffer (*77*) correlated calorific value with chemical analysis and found that the calorific value was directly proportional to the percentage of the original specific gravity retained by the wood. Hilborn (*39*) in evaluating the calorific value of fuel wood when stored under different conditions found the loss in calorific value to be greater than the loss in dry weight. This study was made on wood stored under natural conditions and with many fungi, and thus many types of rot present in the wood. Lehmann and Scheible stated that in pine wood infected with *Armillaria mellea* and *Merulius lacrymans* (Wulf.) Fr. the percentage losses in calorific value were approximately the same as the percentage losses in dry material. Vanin and Esupoff, however, stated that the brown rots tended to raise the calorific value whereas the white rots tended to lower it.

Aliquot parts, approximately 1 gram each, were taken of the wood used in the chemical analysis and the calorific value determined in an Emerson bomb calorimeter. The data are presented in table 18. This table is in general agreement with the results of Scheffer who found that there were no consistent differences in the calories per gram of dry wood as decay progressed. Although slight decreases are shown here in the calories per gram of dry wood in the samples with greater decay, these differences are probably not significant. In other words, the losses in calorific value are directly proportional to the losses in dry weight. As Scheffer points out, it is unfortunate that Lehmann and Scheible did not correlate their calorimetric data with chemical changes, since to have done so might have indicated the calorific value of the different wood components. It is also unfortunate that the losses in calorific value reported by the writer on fuel wood were not

correlated with chemical changes, as in this case numerous fungi were present, and undoubtedly more complex chemical changes occurred than in the other studies, which were conducted with pure cultures under laboratory conditions.

TABLE 18

Calorific Values of Samples of Decayed Wood

Sample No.	Percentage of original dry sound wood according to specific gravity	Calories per gram of dry wood
A	100	4311
B	60	4268
C	40	4162

SUMMARY AND CONCLUSIONS

The list of synonyms of *Fomes fomentarius* (Fr.) Kickx includes about 27 binomials. The fungus has been reported from most of the North American continent, the British Isles, northern and central Europe, China, Japan, and northern Africa. It has been reported on 23 genera and 56 species of trees, mostly hardwoods. In New England, the fungus is practically restricted to *Betula* and *Fagus*, and in Maine the fungus is most common on *Betula populifolia, B. lutea, B. papyrifera*, and *Fagus grandifolia*.

Studies on the morphology of the sporophore showed that the tube layers are stratified. Basidia were found only in the current years' tube layers. At the end of each season the last tube layer is sealed by a sterile hyphal layer which prevents further spore discharge. The spores produced in Maine were larger than those previously reported. The spores from white birch were $25.45 \pm .142 \times 7.33 \pm .025$, and those from gray birch were $22.41 \pm .106 \times 10.34 \pm .126$ microns.

The spore-discharge period for *F. fomentarius* was approximately 180 days. The discharge exhibited three phases, (1) the pre-peak, (2) the peak, and (3) the post-peak. Atmospheric humidity was an influencing factor on spore discharge only during the pre-peak interval. Temperature also influenced spore discharge, and the effect was most pronounced during the post-peak interval. The food reserves of the sporophore apparently influence spore discharge during the peak interval.

Cultural studies showed that there was considerable variation in the time-growth curve for various isolates on the same medium, and for cultures of the same isolate on different media. The group of 28 isolates studied from various sources did not fall into any subgroups based upon the characters studied. There were no indications given by these isolates, from North America and Europe, of the existence of strains or local races within the species. The differences observed were apparently due to individual variation that was independent of either host or locality influence. The range of cultural characters, while great, did not fall outside the characters used to separate *F. fomentarius* from other species in the genus. No significant differences were observed in the reaction of the various isolates to temperature, acidity, or the ability to produce the oxidase reaction on gallic or tannic acid media. All

the 28 isolates studied exhibited mutual aversion when two different isolates were plated together. It is pointed out that a toxin may be formed, or physiological differences may exist, which would cause this aversion, but the data presented are inconclusive.

The fungus destroyed heartwood and sapwood at equal rates in cultures, but different isolates varied in the rapidity with which they destroyed wood from the same source. Isolates also varied in their saprogenicity according to the species of tree from which the wood was secured.

Field studies on infected trees showed that the fungus causes a typical, white mottled rot in the heartwood and sapwood of both living and dead trees. In dead trees the organism apparently attacks the sapwood and heartwood simultaneously as the decay progresses in the tree. In living trees the heartwood is decayed first, and then the adjacent sapwood is invaded. The microscopic characters of the decay showed that the fungus penetrated the cell walls in various ways, and the secondary cell wall was attacked probably following the ramification of the hyphae through the wood parenchyma and wood ray cells.

Chemical studies on decayed wood showed that the fungus attacked lignin and cellulose simultaneously. No differences were found in the utilization of pentosans. A decrease in alkali solubility, characteristic of the white rots, was found. The losses in calorific value of the decayed wood were proportional to the losses in dry weight.

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PLATE 1. Sporophore of *Fomes fomentarius* collected from yellow birch at Old Speckle Mountain, Maine.

PLATE 2. Sections of a sporophore of *Fomes fomentarius* showing the stratified nature of the tubes.

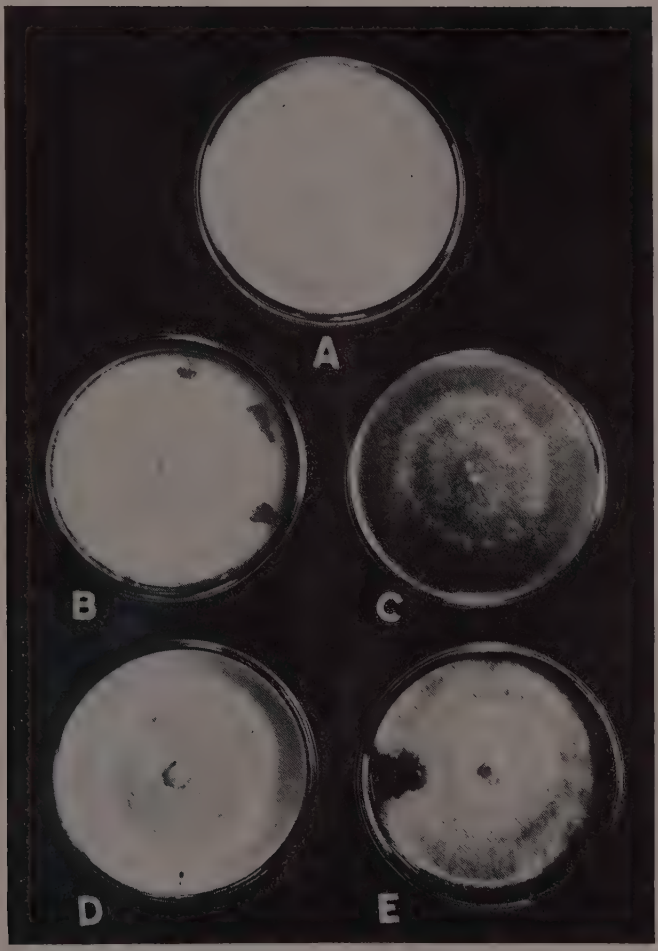

PLATE 3. Mycelial growth of isolate F 1 on different substrata. Photographed after 25 days at 22° C.

A = Leonian's malt extract agar
B = Corn-meal agar
C = Maltose agar
D = Lima bean agar
E = String bean agar

PLATE 4. Mycelial growth of various isolates of *Fomes fomentarius* on Leonian's malt extract agar. Photographed after 25 days at 22° C.

A = F 3309 — White ash—England
B = F 10 — White birch—Maine
C = F 4 — Elm—Maine
D = F 1 — Gray birch—Maine
E = F 6 — Yellow birch—Maine
F = F 2252 — Birch—Canada

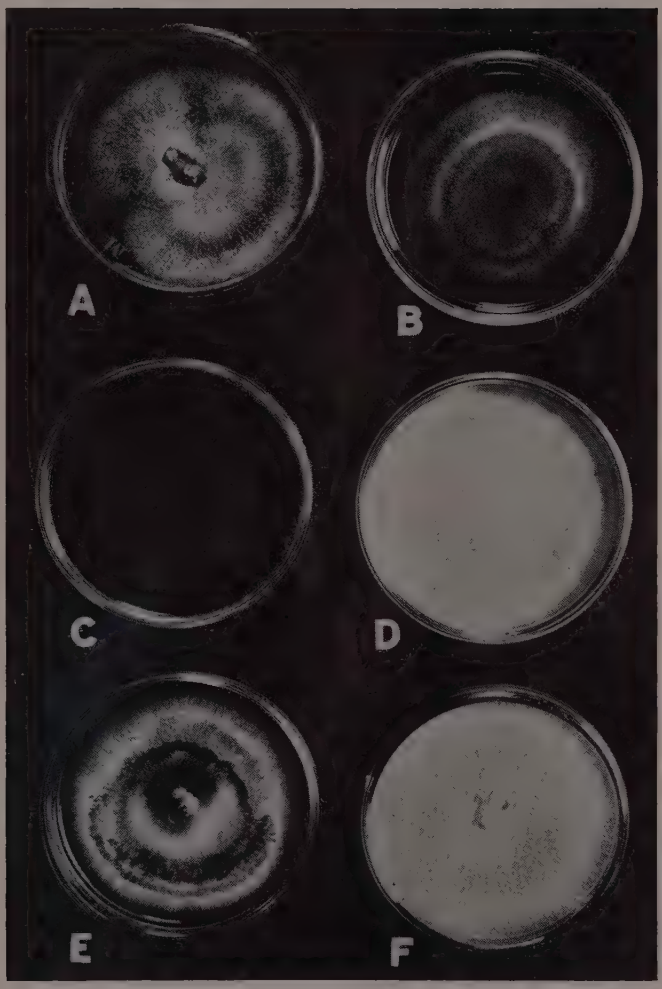

PLATE 4.

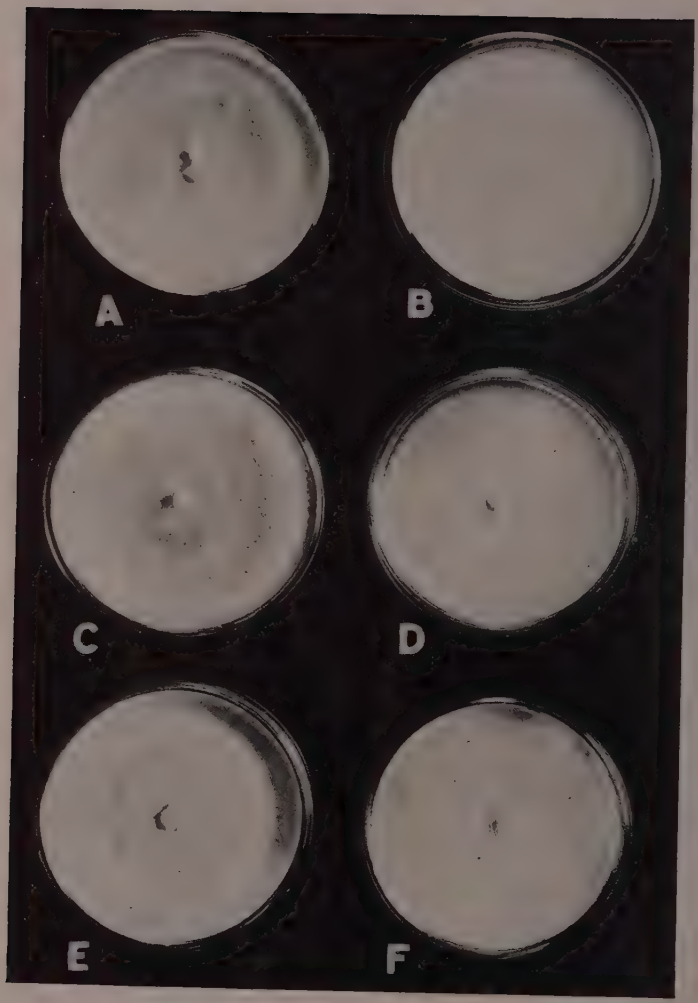

PLATE 5. Mycelial growth of various isolates of *Fomes fomentarius* on lima bean agar. Photographed after 25 days at 22° C.

A = F 1307 — Beech—Canada
B = F 10 — White birch—Maine
C = F 2252 — Birch—Canada
D = F 6 — Yellow birch—Maine
E = F 1 — Gray birch—Maine
F = F 4 — Elm—Maine

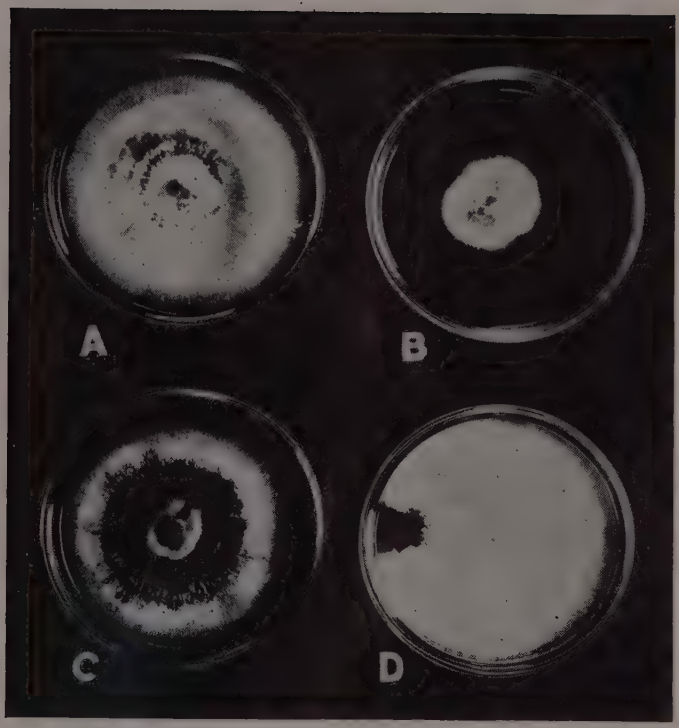

PLATE 6. Mycelial growth of *Fomes fomentarius* on string bean agar Photographed after 25 days at 22° C.

A = F 10 — White birch—Maine
B = F 3309 — White ash—England
C = F 4 — Elm—Maine
D = F 1 — Gray birch—Maine

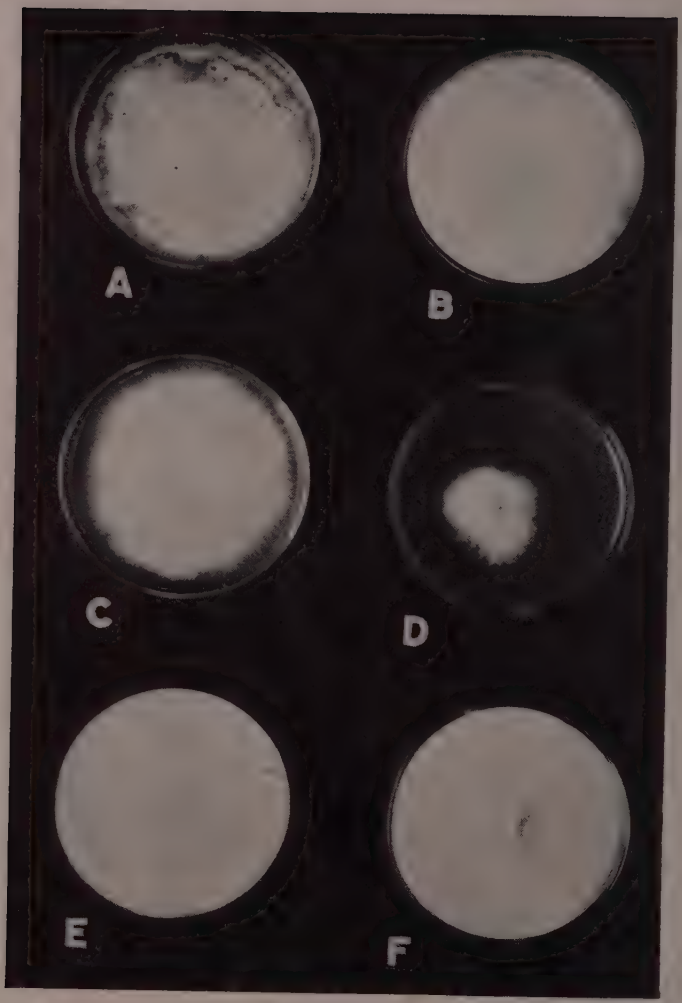

PLATE 7. Mycelial growth of various isolates of *Fomes fomentarius* on string bean agar. Photographed after 15 days at 22° C.

A = 103 — Birch—Scotland
B = 102 — Birch—Scotland
C = 111 — Beech—Austria
D = 105 — Birch—Scotland
E = 206 — Unknown—Germany
F = 197 — Unknown—Germany

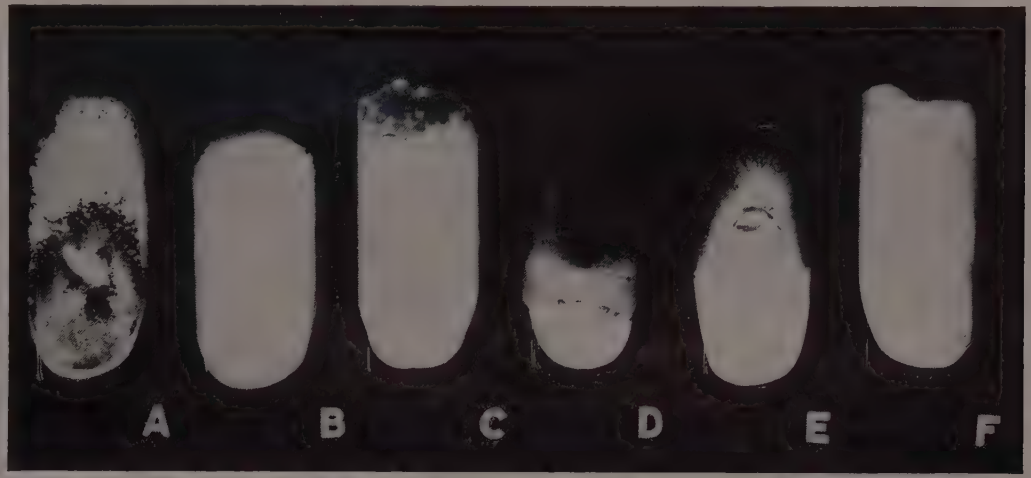

PLATE 8. Mycelial growth of *Fomes fomentarius* on malt agar. Photographed after 35 days at 22° C.

A = F 2252 — Birch—Canada
B = 59100-s — White birch—Maine
C = 57081-s — White birch—Pennsylvania
D = 59011-s — White birch—Minnesota
E = 58572-s — White birch—Minnesota
F = 59012-s — White birch—Minnesota

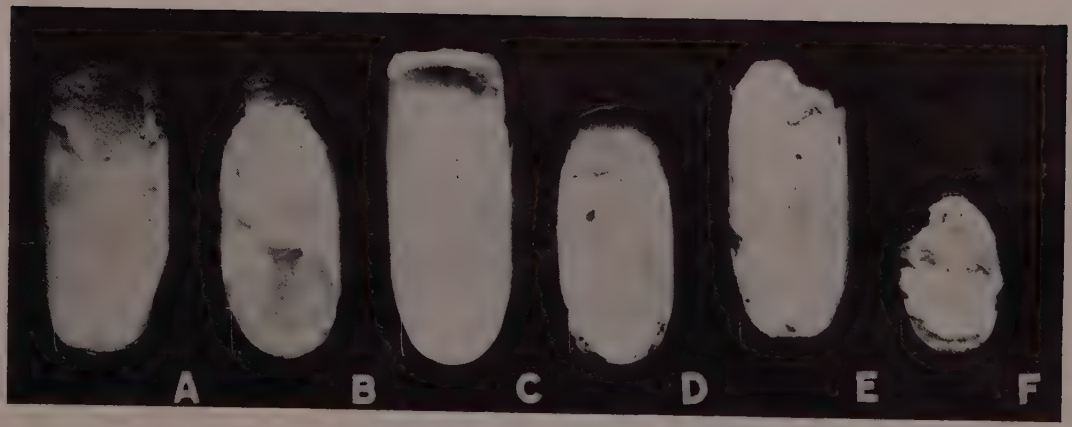

PLATE 9. Mycelial growth of *Fomes fomentarius* on malt agar. Photographed after 35 days at 22° C.

A = 58564 — Beech—New Hampshire
B = F 1307 — Beech—Canada
C = 70960 — Yellow birch—Wisconsin
D = F 6 — Yellow birch—Maine
E = F 9 — Elm—Maine
F = F 4 — Elm—Maine

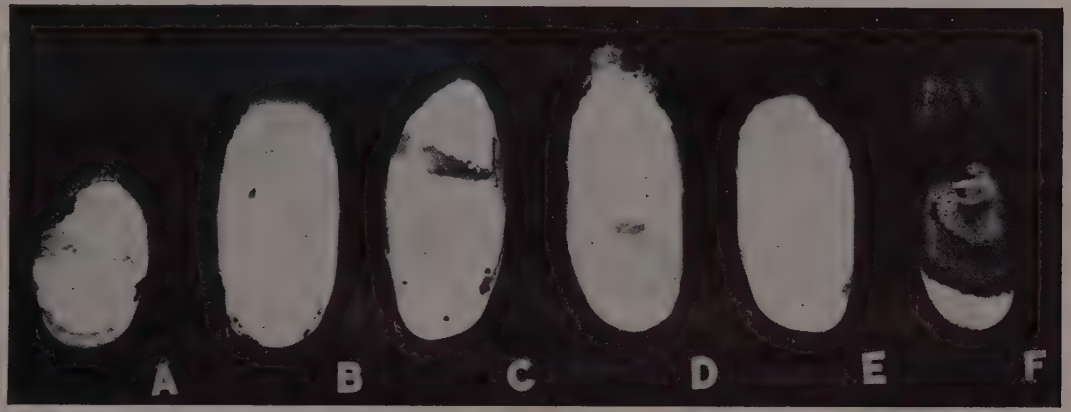

PLATE 10. Mycelial growth of *Fomes fomentarius* on malt agar. Photographed after 35 days at 22° C.

A = F 4 — Elm—Maine
B = F 6 — Yellow birch—Maine
C = F 10 — White birch—Maine
D = F 1307 — Beech—Canada
E = 59010-s — Aspen—Minnesota
F = 70957 — Maple—Wisconsin

PLATE 11. Comparison of five pairs of cultures as follows: Note line of demarkation in A, B, C, and D, and absence in E.

A = 58572-s — White birch—Minnesota (upper half)
59012-s — White birch—Minnesota (lower half)
B = F 1 — Gray birch—Maine (upper half)
F 9 — Elm—Maine (lower half)
C = 58572-s — White birch—Minnesota (upper half)
58564-s — Beech—New Hampshire (lower half)
D = 57081-s — White birch—Pennsylvania (upper half)
59013-s — White birch—Minnesota (lower half)
E = 59011-s — White birch—Minnesota (upper half)
59011-s — White birch—Minnesota (lower half)

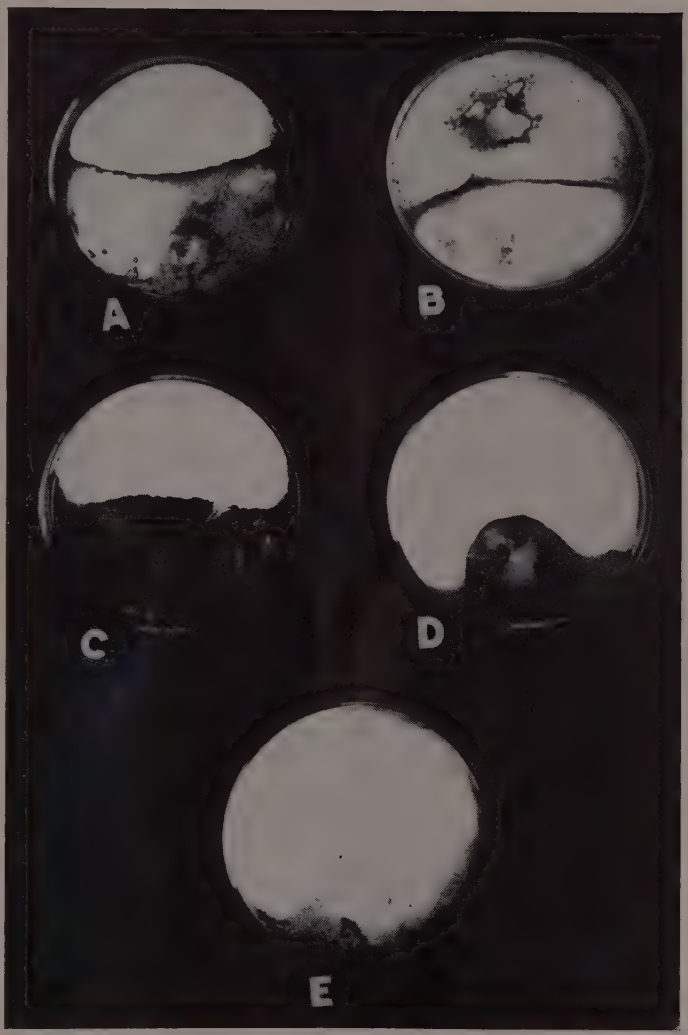

PLATE 11.

PLATE 12. Comparison of six pairs of cultures as follows: Note line of demarkation in A, B, C, D, and F, and absence in E.

A = 59013-s — White birch—Minnesota (upper half)
F 1 — Gray birch—Maine (lower half)
B = 57081-s — White birch—Pennsylvania (upper half)
59011-s — White birch—Minnesota (lower half)
C = 59012-s — White birch—Minnesota (upper half)
59011-s — White birch—Minnesota (lower half)
D = 58572-s — White birch—Minnesota (upper half)
57081-s — White birch—Pennsylvania (lower half)
E = 59009 — Aspen—Minnesota (upper half)
59009 — Aspen—Minnesota (lower half)
F = 57081-s — White birch—Minnesota (upper half)
59013-s — White birch—Minnesota (lower half)

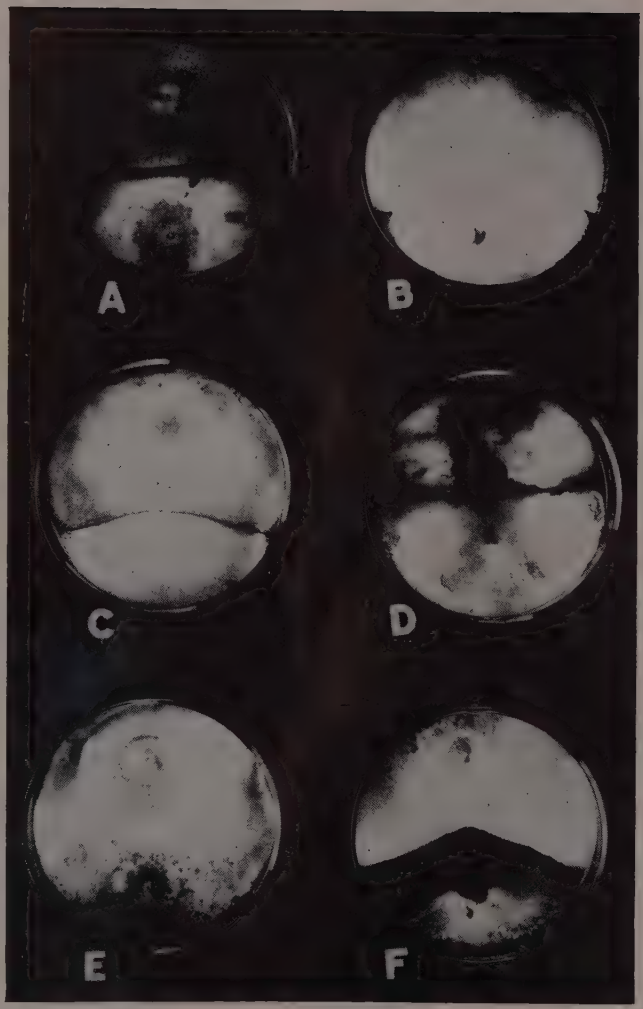

PLATE 12.

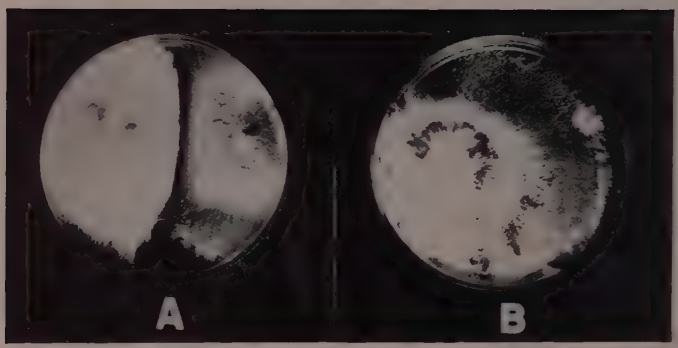

PLATE 13. Absence of effect of plating one isolate against the liquid malt extract upon which an antagonistic isolate had been grown.

A = 59012-s (left) and F 9 (right)
B = F 9 plated against centrifuged and filtered extract upon which 59012-s had been grown.

PLATE 14. *Fomes fomentarius* on blocks of yellow birch in quart Mason jars. Isolate F-4 after 8 months incubation.

PLATE 15. Five of the 4-foot bolts from the White birch tree examined at Sieur De Monts Spring, Acadia National Park. At left is the basal 4-foot bolt; second, the 4-foot to 8-foot bolt; third, the 8-foot to 12-foot bolt; fourth, the 12-foot to 16-foot bolt, and at the extreme right, the 16-foot to 20-foot bolt. Due to a splitting of the decayed wood the top part of the 16-foot bolt was lost resulting in an obvious discrepancy in the width of the healthy sapwood at the top of the 16-foot bolt and the bottom of the 20-foot bolt.

PLATE 16. Two stages in tangential view of the decay produced in white birch by *Fomes fomentarius*. The two blocks at the left show the intermediate stage and the two at the right the advanced stage.

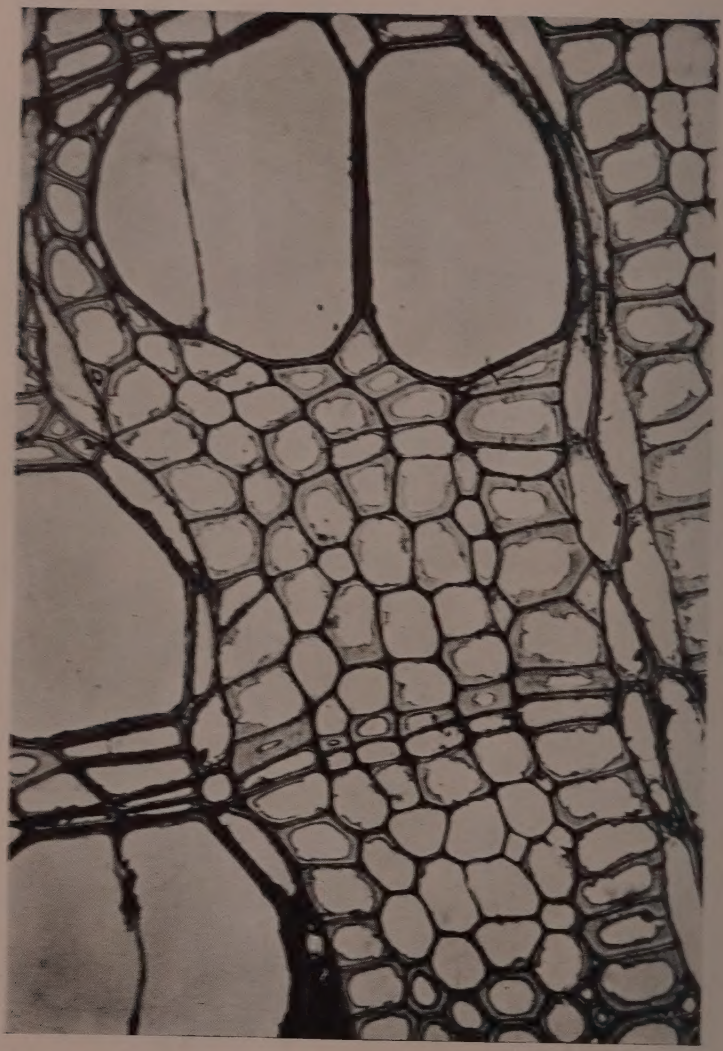

PLATE 17. Cross section of white birch showing the decay caused by *Fomes fomentarius* approximately 800x.

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